Individual assessments and collective decisions

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INDIVIDUAL ASSESSMENTS AND COLLECTIVE DECISIONS

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For my Ma and Da

Abstract

INDIVIDUAL ASSESSMENTS
AND COLLECTIVE
DECISIONS

Leptothorax albipennis ant colonies face a difficult task when their ephemeral nests are destroyed in the wild. There they are a collection of less than 500 relatively puny brown ants, completely exposed to their harsh environs. Before the colony is eaten or blown away, scouts must go out and find a new suitable nest, among many alternatives. Then they must let the other workers know about this new nest.

How do the ants measure a nest? Experiments show that individual ants can estimate relatively large areas with considerable accuracy by deploying individual-specific trail pheromones and by relating the number of intersections between their current path and their previous path to nest area. The logic of this algorithm is identical to a method proposed to estimate π empirically, developed two centuries ago by Comte George de Buffon.

How does the colony integrate all the measures (different ants may visit different nests) so that it chooses only one nest? I found that although individual ants can compare both nests, most scouts see only one nest. How do they contribute to the decision? Several aspects of individual behaviour were examined to see did these behaviours lead to the colony choosing a superior nest. Neither the number of recruiters, the amount of recruitment carried out by an individual nor the rate at which it performs that work is different when an ant recruits to a superior nest as opposed to a mediocre one. Rather, what is fundamental is the likelihood, after assessing a nest, that a scout will begin to recruit to this nest. The initial early preference coupled with the two-phase recruitment process allows the colony to make a consistent unanimous decision.

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ACKNOWLEDGMENTS

I would like to thank Nigel Franks for the many ways in which he contributed to this project. Not only did he come up with the initial idea, he also found the funding. No small achievement considering British funding bodies dislike of foreigners. We have written numerous manuscripts together; chapter four especially borrows heavily from two of our manuscripts. The magic carpet experiment was wholly Nigel's idea.

I wish to use this opportunity to proclaim a debt of gratitude to Stephen Pratt. I am indebted to Stephen not only for his considerable guidance and practical support, but also for his garrulous co-experimenting. Without this relief, I'm sure not nearly as many replicates would have been completed. Stephen and I performed the two-camera experiment together. He also aided in the initial analysis of my one-camera experiment. Chapter 5 is based on a manuscript that we have written together.

Thanks to the numerous undergraduates who were co-supervised by me. Special thanks to Sam Mugford for his work on the accuracy of Buffon's needle which appears in Chapter 4.

A final and sincere thanks to the various encumbents of the ant lab during my tenure there; Ana, Guy, Iain, Jay, Mel, Liz, Sarah, and Speny. I think together we made the ant lab one of the most friendly if not the most serious labs in Bath.

While at Bath, I was sponsored by a Natural Science Demonstratorship provided by the biology and biochemistry department.

Chapter 1

INTRODUCTION

The roof comes off again. The ants seem suddenly very naked in a harsh environment. The brood must be protected. The queen must be saved. A new home must be found, assessed and chosen from among all possible sites. How colonies of the ant *Leptothorax albipennis* carry out this minor miracle of logistics is the subject of this thesis. Why would anyone be interested in this? This is a question that although I never asked myself (a sign of an ungrasping mind perhaps?), has been asked of me often, usually in the pub by an accountant. I could answer in one of two ways. Actually answer the question, describing for them in detail the joy of discovering Nature's arcana or even that general principles may come out of the research which have a utilitarian bent (which is what they really mean). However this strategy sets me up as a pompous bore. My grandda always said never talk about politics; religion or sport in the pub, to that I would add myrmecology. So I usually plump for the second option, which is to change the subject or offer some trite explanation ("its better than walking the streets"). My accountant friend now knows I am a moron with a mad job.

However today is different. Today, I will try to explain why I (and reciprocally you) should be interested in how a small colony of less than 500 individuals (not for *Leptothorax* the gaudy showiness of millions of workers), assesses a new nest, decides among alternative ones, and then moves itself into its chosen home.

The behaviour of groups, whether they be groups of molecules, *Myrmica* or men are intriguing because out of their apparent individual randomness comes a group behaviour that is consistent and regular. People make whole careers out of understanding how, from the petty biases, arguments and limitations of consumers, comes a clear decision to prefer Coke to Pepsi or VHS over Betamax. It is the process of collective decision-making that interests me.

Ants are an interesting group with which to study collective decisions. For decades, colonies of social insects have been seen, almost romantically, as being not a mere loose conglomeration of individuals but rather a superorganism (Wheeler 1928; Wilson and Sober 1989). A superorganism - a group so closely

integrated that they can be seen as analogous to a single organism, making them the latest major transition in evolution (Maynard Smith and Szathmary 1997). Social insect colonies possess remarkable abilities to select the best among several courses of action (Bonabeau et al. 1997; Camazine et al. 1999; Detrain et al. 1999). In populous societies with highly efficient recruitment behaviour, decision-making is distributed across many individuals; each acting on limited local information with appropriate decision rules (Franks et al. 1991).

An excellent example of this ability is how *Lasius niger* colonies reliably choose the shortest path to food during a laboratory experiment (Beckers et al. 1992). As shown in Figure 1.1, the food source is separated from the colony by a space that can be crossed by two bridges, a short and long one. The ant lays trail pheromone on its way to and from the food source. This pheromone attracts other ants, the higher the level of pheromone the more attractive it is to the ants. The pheromone very slowly evaporates. Initially each forager chooses at random which bridge to cross. However, ants that use the shorter path return more quickly to the colony and so can make more trips. Eventually the shorter path is more heavily marked with trail pheromone than is the longer path. Now ants approaching the two bridges will be attracted more to the shorter bridge. Eventually almost all the traffic will be on this shorter bridge. The colony has decided to use this bridge. But it made this decision without it being necessary for a single ant to examine both paths. Rather it is the interplay between recruitment and travel time that leads to the collective selection of the shortest path.

This is an example of a positive feedback mechanism and this process is, of course, not restricted to ants or social insects. It is one of the basic processes

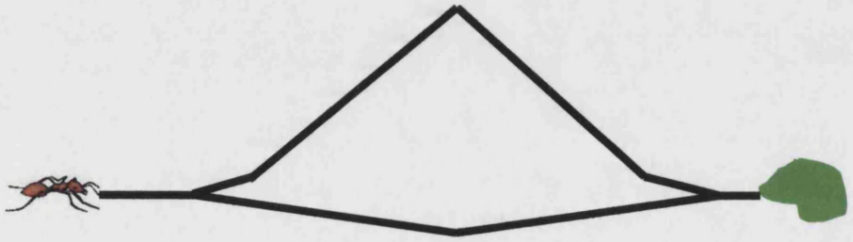

Figure 1.1 A diagram showing the set up for path length decision. The green area represents the food source.

involved in self-organisation. Self-organisation is the idea that complex collective behaviour can be explained by the interactions among individuals that exhibit simple behaviours (Bonabeau et al. 1997). The idea originally comes from physics where it was used to describe how microscopic processes give rise to macroscopic structures in out-of-equilibrium systems (Nicolis and Prigogine 1977). It has found favour in many different fields, apart from social insect research, notably computer programming (Bonabeau and Theraulaz 2000), business management (Santosus 1998), economics (White 1996) and neurobiology (Gerhart and Kirschner 1997). I would not suggest to my accountant inquisitor that studying ant social behaviour will lead directly to answers in any of the previous fields, but rather from it could come general principles about how groups behave that could be applied to other fields. As an example, ant-like algorithms (ALA) (Bonabeau and Theraulaz 2000) are a hot topic in computer programming. Principles from ant foraging, specifically, have allowed computer programmers to look at difficult computational problems, such as the travelling sales man dilemma, from new angles.

In the travelling salesman problem, a traveller must find the shortest route to visit a finite number of cities, each only once (Bonabeau and Theraulaz 2000). This problem is very difficult to solve; for fifteen cities there are billions of possible routes. The travelling salesman problem is a theoretical example of a general class of problems (nondeterministic polynomial complete) that are of great interest to computer programmers and telecommunication engineers. Researchers have unleashed swarms of artificial 'ants' onto the travelling salesman problem (Dorigo and Gambardella 1997).

Each individual ant travels independently from city to city, favouring nearby cities but otherwise moving haphazardly. After visiting all the cities the ant retraces its steps, this time laying a pheromone trail. The amount of pheromone is inversely proportional to the overall length of the ant's journey. After all the ants have finished, the links most involved in the shortest route will have the highest

amount of pheromone. If the colony is again allowed to explore this virtual collection of cities and this time the ants are attracted to the links with the highest level of pheromone moderated by the inter-city distances, then the colony will use a route that is one of the shortest (although not necessarily the absolute shortest) routes. How much of an improvement this method is over current methods is a debate that is best left to computer scientists. It does show, however, important work in a different discipline based on insights gained from the study of ant social behaviour.

The principles, taken from social insect research by other fields, have come entirely from examples of populous societies with highly efficient recruitment behaviour, just as in the example of path selection above. This is because, thus far, these examples have been studied the most intensely. Decision-making by small societies with rudimentary recruitment is much less well studied. To what degree could these societies employ distributed decision-making? What additional processes are involved to allow them to make a decision?

Nest choice by *L. albipennis* is an example of this decision-making by small colonies. A colony of *L. albipennis* housed in an artificial nest is shown in Figure 1.2. The Leptothoracine ants belong to the tribe *Formicoxenini*, part of the

Figure 1.2 A painted *Leptothorax albipennis* colony.

subfamily Myrmicine (Bolton 1994). There are two principle subgenera, *Leptothorax* (*Myrafant*) and *Leptothorax* (*Leptothorax*). The current species formerly called *Leptothorax tuberointerruptus* (Orledge 1998) belongs to the *Myrafant* subgenera.

The species has monomorphic workers. Colonies are monogynous, each with a singly mated queen. *L. albipennis* colonies in Britain nest naturally in cracks in rocks (Partridge et al. 1997). The ants can only alter these crevices minimally by building small dirt walls. They are thought to be primary predators and scavengers of other invertebrates. The emigration behaviour of other *Leptothorax* species has been studied previously (Moglich 1978). Scouts go out and begin assessing potential new nests. A scout returns to the old nest and lifts up its gaster releasing a 'tandem calling' pheromone (Moglich 1979). Nestmates are attracted by this pheromone. One nestmate is then led, in what is called a tandem run (Figure 1.3), from the old nest to the new nest. The follower keeps in constant antennal contact with the gaster of the leader. If contact is broken, then the follower begins a stereotyped search pattern for the leader, who waits, motionless, for contact to be resumed. If contact is not re-established within a set time, the two participants give up and often begin again with a different partner. Eventually a critical number of workers is reached in the new nest and tandem running ceases. Many of the original discoverers and tandem-lead ants now begin physically to carry other workers (Figure 1.4) and brood from the old nest to the new nest. Concurrently, a number of reverse tandem runs are seen from the new nest to the old nest.

This recruitment method is very different from that of mass recruitment ants where reinforced pheromone trails are used (Hölldobler and Wilson 1990). How do these small colonies make decisions? One possibility is that distributed decision-making is supplemented by individual decision-making. Individual ants could compare both nests. This possibility is examined in chapter five.

The individual abilities of ants are not limited to this possible role in decision-making. The decision to move into a new nest is based on the assessment of

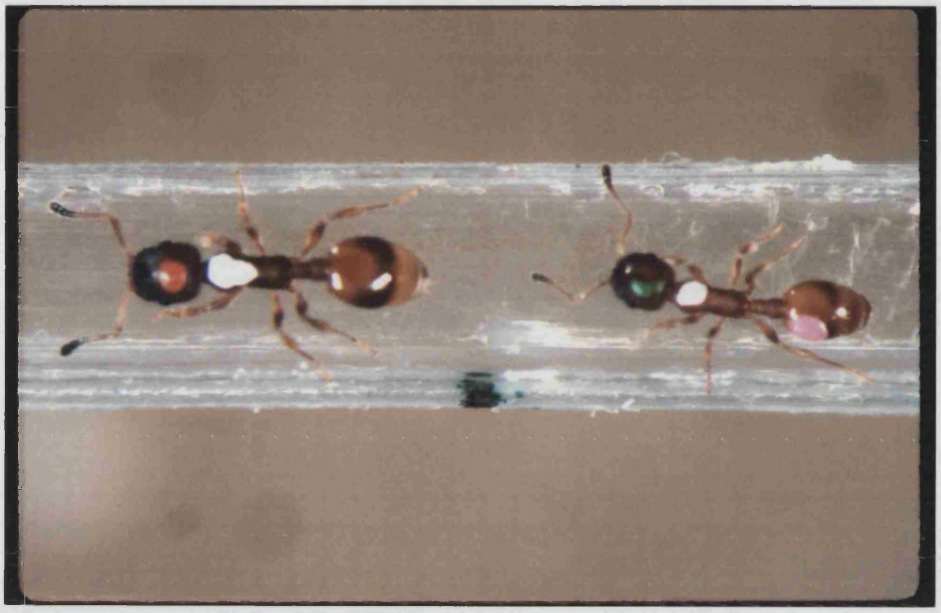

Figure 1.3 Two ants involved in a tandem run, unfortunately just momentarily separated. Photo courtesy of S.C. Pratt

Figure 1.4 Carrying Behaviour. Photo courtesy of S.C. Pratt

nests that is made by individual ants. What variables are important to colonies and how do the individual ants assess them. This assessment ability of animals is, I feel, an under researched area of behavioural ecology.

Chapter 2 begins the study of decision-making by looking at the process from an organisational point of view. Do colonies make consistent decisions? How 'intelligent' does the colony need to be to make a decision? How many attributes of a nest does a colony examine when deciding on a nest? How does the colony compare and trade-off these various attributes?

Chapter 3 and 4 are concerned with how the individual ants assess the nest. Out of all the possible attributes, the assessment of the area of the nest was studied. Although other attributes would not be trivial for an ant to measure, I thought that this size quantity would be the most difficult to estimate, due to the fact that the space being examined is much larger than the size of a single *L. albipennis* worker. Chapter 3 looks at the possibility of pheromones being involved in this assessment process. Chapter four tests several algorithms that could be used by ants to measure the area of the nest.

Chapter 5 concerns itself with how these individual assessments are turned into a collective decision. What behaviour by the individual ants leads to the whole colony choosing a single nest? This is the central topic of the thesis and brings us back to where we started, trying to understand group behaviour as the accumulation of the relatively simple individual behaviours of the group members.

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Chapter 2

NEST CHOICE AND DECISION MAKING STRATEGIES

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2.1 Introduction

Animals have to make decisions all the time, probably even more than Snoopy's one hundred and twenty a day. They must decide about when and where to forage, when and with whom to mate, when to start and stop fighting. Often these decisions would be hidden to an observer. When an animal continues to forage, how many decision points between continuing and stopping have been crossed since its last obvious decision point, when it started foraging? To say that an animal makes decisions implies no conscious intent but merely refers to the fact that the animal takes one behavioural alternative rather than another.

In ecology, decision making by animals is considered in one of two ways: functional or mechanistic. Functional explanations are often in the form of optimality models (see below). They have as their starting point what an animal ought to do to achieve the best outcome. Mechanistic models look at how an animal makes a decision, that is, what are the proximate causes of its decision.

2.1.1 Optimality theories

In a branch of economics known as utility theory, decisions are represented as being based on which alternative action will bring the actor the most 'utility'. Utility is defined, circularly, as that value which the actor, usually a consumer, wishes to maximise. Ethologists have recognised that if animal behaviour is studied from an evolutionary viewpoint then utility is comparable to inclusive fitness (McFarland 1985). If an animal behaves optimally then it is working to maximise its inclusive fitness. Decisions therefore can be analysed in terms of an optimal trade-off between appropriate costs and benefits.

Kacelnik (1984) has studied animal decision-making in this way. He looked at the foraging patterns of nesting starlings. Kacelnik found that the parent calculates carrying loads by trading off the ease of capture of food due to the amount of food already in its mouth and the distance it must fly to the foraging site. This chapter does not deal with the optimality of the nest choice decisions made by *Leptothorax albipennis* colonies (see Discussion). Such work would require the field

estimation of many variables of colonies' life history traits. The above discussion of optimality was merely presented to alert the reader to the type of work that has been carried out previously on decision-making in animals. I decided to look at decision-making from a completely different angle.

2.1.2 The cognitive abilities of an ant colony

I am interested in the cognitive abilities of an insect colony. Just how clever is the superorganism? An entire social insect colony can act as single unitary problem solver. That is, it is capable of making adaptive decisions. Mental effort has a long and venerable history as a theoretical construct in psychology (Kahneman 1973; Navon and Gopher 1979; Thomas 1983; Hockey et al. 1986). The idea that decision-making is influenced by considerations of cognitive effort is an old one (Simon 1955; Marschak 1968). It would seem obvious that different decision-making strategies (see below) require different amounts of computational effort.

The 'test' of computational effort that I gave the colonies was the choice between two (sometimes three) nests of different quality. Do *Leptothorax albipennis* colonies make consistent decisions about where to live? What decision-making strategy is being used to make this decision. The ability of animals to make decisions about where to live is crucial to their fitness (Lack 1968; von Frisch 1974; Seeley 1985a). Many animals have the ability to discriminate among nesting sites or among territories on the basis of quality. Rendell and Verbeek (1996) showed that the nest cavity choice of the tree swallow is influenced by the amount of debris remaining from previous inhabitants, as this affects both the size of the cavity and the abundance of ectoparasites. Cliff swallows consider the time it would take them to build a nest at a new site the most important factor in site selection (Gauthier and Thomas 1993). Honeybees have been shown to discriminate between potential nest cavities based on many different variables including volume of the nest cavity, presence or absence of comb and height above the ground (Seeley 1977). The computational aspects of decision-making (Payne et al.

1993) are therefore an excellent way to examine the computational abilities of insect colonies.

Decision-making is sensitive to such task factors as number of alternatives and attributes, time constraints, and information format (i.e. is it a straight choice or is it a situation where alternatives are to be rated separately etc.?). It is also highly sensitive to context. Context includes the similarity of the options in a choice and the reference points that the decider would use. The importance of such task and context effects may create a view of decision-making behaviour as inextricable (Hogarth 1992). However generalisations about decision behaviour have emerged. Many different decision-making strategies have been identified. They range in both their accuracy and the computational ability required to carry them out. Some of the more common ones are outlined below.

2.1.3 Decision making strategies

2.1.3-1 The weighted additive strategy

This strategy considers the values of each alternative with regard to all the relevant attributes and considers the relative importance or weight of each attribute. It involves the calculation of a single abstract quantification of each alternative's desirability. These values are then compared to each other.

2.1.3-2 The equal weight heuristic

This strategy examines all the alternatives and all the attribute values for each alternative. However, the equal weight strategy simplifies decision making by ignoring the relative importance of each attribute.

2.1.3-3 The lexicographic heuristic

This method determines the most important attribute and then examines the values of all alternatives on that attribute. The alternative with the best value according to the most important attribute is selected. With this heuristic, each alternative is compared stepwise for each attribute (most important to least important) until a single alternative can be distinguished from the others.

2.1.3-4 The elimination by aspects heuristic

Here the process begins with a determination of the most important attribute. Then, any alternative with a value of this attribute below a cut-off point is disregarded. Next, the second attribute is examined and so on till only one alternative is left. The important difference between this and the previous heuristic is that with this heuristic, decisions are made based on cut off points, that is decisions are series of binary choices rather than selecting the best alternative (lexicographic heuristic).

2.1.3-5 The satisficing heuristic

This is similar to the elimination by aspects heuristic, except here the elimination process does not continue until only one alternative is left. The alternatives are considered one at a time in the order in which they are found. The process ends as soon as one of the alternatives matches or exceeds a cut-off valve for the currently examined attribute.

Which decision-making strategy is being used by the ant colonies? A first step in answering this question is to work out what attributes of a nest site are important to the colonies. I decided to limit the variables to those to do with the structure of the nest. This is because these variables are easily manipulated and measured unlike certain variable such as temperature that would require some equipment to keep each prospective nest at a different constant temperature. Area, on the other hand, is easily manipulated, the nest just needs to be cut to the right size, and area is easily measured. Once the important attributes have been discovered, the relative importance of these attributes can be compared, using different combinations of nest type. This will elucidate which particular strategy is being used by the ant colonies to make a decision.

2.2 Methods and Results

2.2.1 Collection and culturing of colonies

Up to twenty colonies of *Leptothorax albipennis* were collected each spring at a disused quarry on Portland Bill, Dorset (see Figure 2.1). They were cultured in the laboratory by housing each colony in a nest made by sandwiching a piece of cardboard between two glass microscope slides (Sendova-Franks and Franks 1993). The nesting cavity within the cardboard was 38mm x 24mm x 0.8mm. This is the 'old standard' nest. The 'old' refers to the fact that due to a change in the camera used for experiments the standard dimensions of the house nest were altered slightly. The single entrance way to the cavity measured 4mm x 4mm x 0.8mm. Each nest was placed in a petri dish, 100mm x 100mm x 17mm, the walls of which were covered with Fluon® to prevent the ants escaping. Except during experiments, the colonies were fed *ad libitum* with *Drosophila* larvae, honey water and water.

2.2.2 General protocol for nest choice experiments

The experimental arena was a large (220mm x 220mm) square petri dish, the sides of which were covered with Fluon®. The new nests were all placed 10cm away

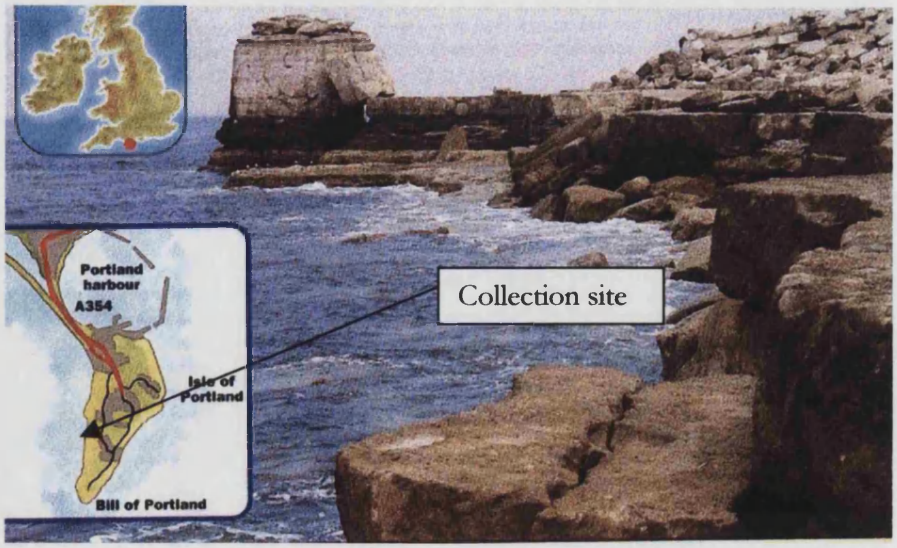

Figure 2.1 The location of the collecting site

from the old nest (entrance to entrance). This distance was found to be large enough to allow a clear decision between nests to be made and small enough to view the whole emigration. The emigration was initiated by placing the old nest in the arena and removing the uppermost glass slide from the old nest (Sendova-Franks and Franks 1993). Each colony was only emigrated once for each particular choice. The relative positions of the different sized nests were randomised so as to eliminate the effects of any directional bias, which the ants might have. The size and design of nests used is shown in Figure 2.2. After initiating the experiment, the colonies were then left for two days. A colony was deemed to have chosen a nest when all ants bar a few foragers were inside this nest. A binomial test was performed on each data set to determine if the results differ significantly from a random choice.

2.2.3 Nest area

2.2.3-1 Do colonies make consistent decisions?

This whole thesis would be a non-starter if I found that the colonies did not, in fact care what size of nest they lived in. The choice given in this experiment was between an 'old standard' nest (38 mm X 24mm X 0.8mm with a nest entrance 4mm X 4mm) and ones which were half (26mm X 16mm) and double (52mm X 31mm) this size. Figure 2.3 shows the number of colonies that chose each type. The colonies seem to reject the $^1/_2$ old standard nest. Presumably it is too small for their needs. To test if this was significant, I combined the results for the 'old standard' and 2 'old standard' nests ($p = 0.000244$).

2.2.3-2 An upper size limit

The colonies have no preference between the 'old standard' nest and one twice as large. I offered them a choice between the former and a nest four times as large. 11 colonies chose the 'old standard nest' and six chose the 4 times 'old standard' ($p = 0.094421$). So up to this size the colonies have no preference. I couldn't test any bigger sized nest due to a limit on the size of the microscope slides and

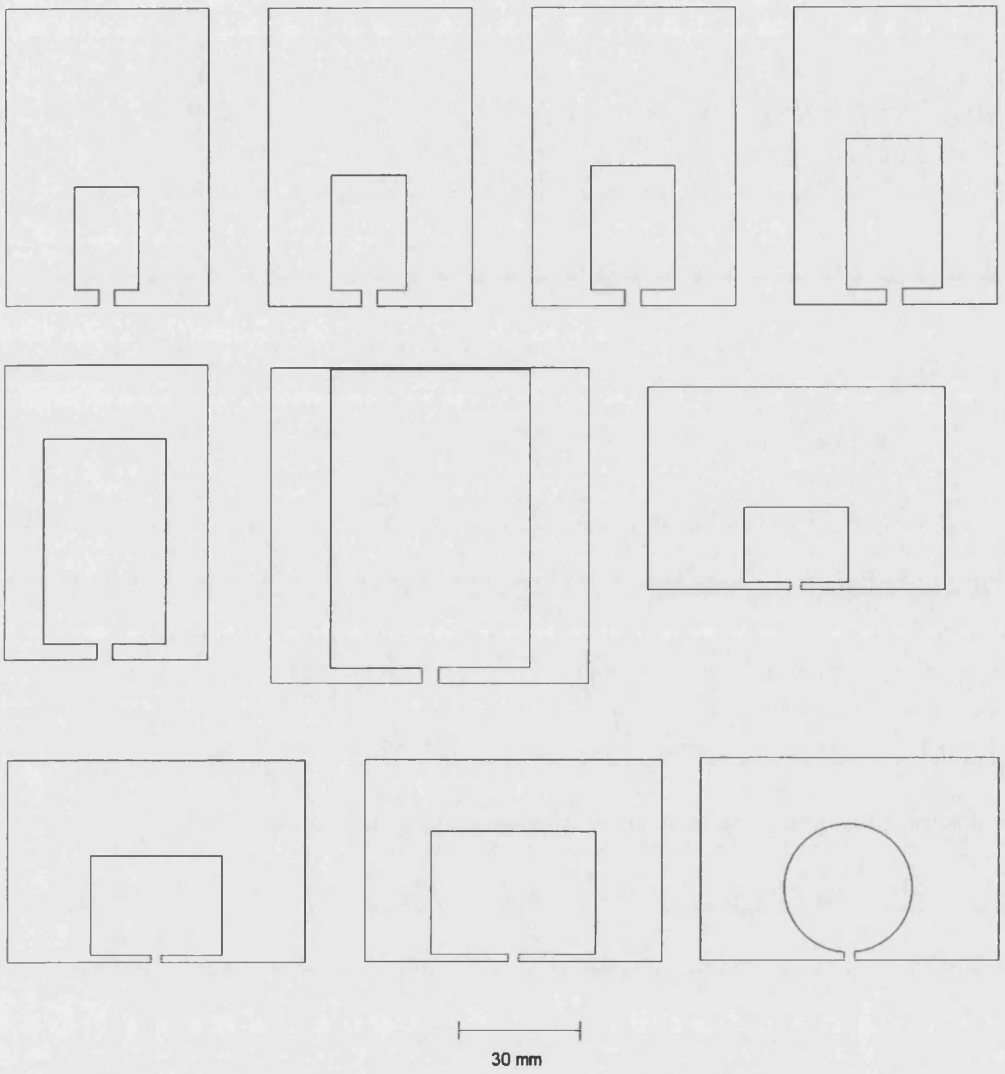

Figure 2.2 The various nest designs used in this chapter. From left to right; 1/2 'old standard' (OS), 5/8 OS, 3/4 OS, OS, 2OS, 4OS, nest for Small colony, 'new standard' nest, nest for Big colony and circular standard nest.

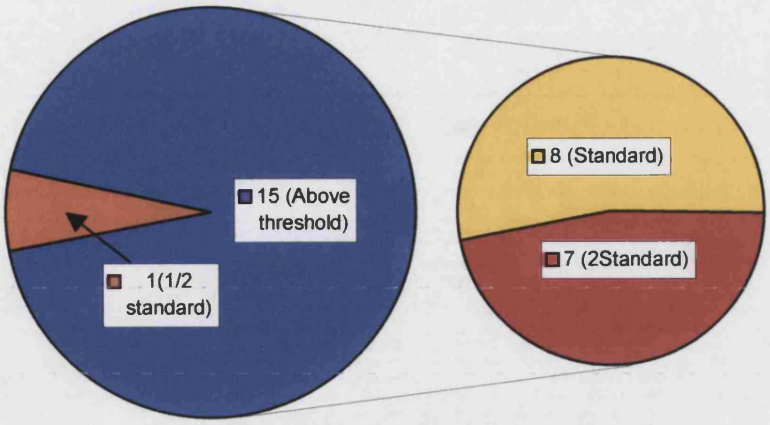

Figure 2.3 A pie chart showing the number of colonies that choose each type of nest. Old Standard and twice old standard were combined to create the category 'Above threshold'.

experimental arenas I could obtain (see Discussion).

2.2.3-3 The precision of nest area measurement.

The colonies can reject half-sized 'old standard' nests in preference to 'old standard' nests. Can the colonies select an area on a finer scale? Two simple choices were presented to the colonies (1) an 'old standard' nest and one ¾ this area (21mm X 31 mm) and (2) an 'old standard' nest and one $^5/_8$ this size (19mm X 29mm). Eight out of fifteen colonies choose the ¾ 'old standard' nest. The colonies therefore do not differentiate between a ¾ 'old standard' nest and an 'old standard' nest. Fifteen out of fifteen colonies chose the 'old standard' nest when it was offered with a $^5/_8$ standard nest. This $^5/_8$ nest is too small for their needs. The colonies lower size limit is somewhere between $^5/_8$ and ¾ 'old standard' nests. The colonies have a resolving power of at least one eighth an 'old standard size', that is 114mm^2.

2.2.3-4 The effect of colony size on nest choice.

It could be imagined that the size of a colony would have an effect on the nest choice of that colony. The larger the colony the larger would be its minimum acceptable nest area. I divided thirty colonies into two groups; Big colonies (> 100 workers) and Small colonies (< 100 workers). Franks et al. (1992) discovered that these ants allow themselves 5mm^2 per ant when building internal walls. A nest 26mm X 19mm (nest entrance 2mm X 2mm) should fit any of the small

colonies. The biggest Big colony was 251 workers. The Big nest was made to accommodate this number (41mm X 31mm).

Figure 2.4 shows the results when each colony was offered the choice between a Big nest and a Small nest. There was no difference in the number of times different sized nests were occupied by the different sized colonies (Fisher's exact test: $p = 0.6485$). It is intriguing that the Big colonies seem to split more often.

2.2.4 Nest entrance width

It is well known that this species of ant will use any material it finds to try and reduce the size of the entrance. Do colonies prefer smaller nest entrances? The colonies were offered the choice between a 4mm wide and 1mm wide entrance (the nests were 'new standard' nests, 25mm X 33mm X 0.8mm). Ten colonies out of thirteen chose the 1mm entrance ($p = 0.0349$). Therefore, colonies prefer the 1mm nest entrances.

2.2.5 Nest height

The first choice was between an 'old standard' nest and a nest of the same dimensions except with a height of 2.4mm rather than 0.8mm. There was no significant difference between the number of times each nest was chosen (5 for

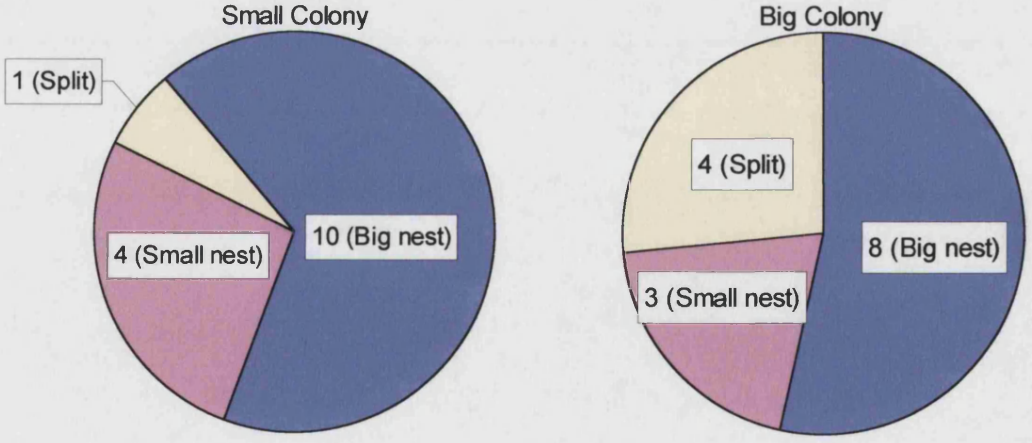

Figure 2.4 the number of the different sized colonies that choose each type of nest

the 2.4 mm and 9 for the 0.8mm, p = 0.122192). The following year I offered different colonies a choice between a 'new standard' nest and a similar nest with a height of 1.6mm. The colonies overwhelmingly choose the 1.6mm nest (1.6mm =12, 0.8mm = 0, p = 0.000244).

It is possible that it is not the nest cavity height that is important, but rather the nest entrance height. To test this, I gave the colonies a choice between a 'new standard' nest (height = 0.8mm) and one with a nest cavity height of 1.6mm, but a nest entrance height of 0.8. This nest was made by joining together two nests with a height of 0.8mm, but only one of them having an entrance. The one without an entrance went on top so as not to obstruct ants as they came and went (see Figure 2.5). If the colonies were interested in nest entrance height, then both nests would have been equally suitable, so I would have expected an even number of colonies to have chosen either nest. Twelve colonies out of twelve chose the nest with the 1.6mm nest cavity, so it is nest cavity height rather than nest entrance height that is important to a colony.

2.2.6 Nest shape

I gave the colonies a choice between a 'new standard' nest and one of the same area and height but which is a circle rather that a rectangle. Sixteen out of twenty six colonies chose the circle, this is not significantly different from a random choice (p = 0.079151).

2.2.7 Brightness of nest

Although normally nests are left uncovered, if someone in the lab is trying to encourage a stubborn colony to emigrate, they cover the new nest. The colony

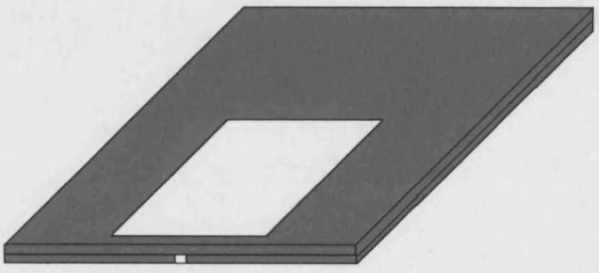

Figure 2.5 The nest used in the nest entrance

moves straight in, no great surprise considering ants' normal desire for the dark. To quantify this phenomenon, I offered the colonies a choice between a 'new standard' nest and the same type of nest with a piece of card on top to block off the light. Fifteen out of fifteen colonies chose the darker nest.

2.2.8 Decision making strategy

Colonies will move into the 0.8mm nest but prefer the 1.6mm nest when offered it. They do the same when offered the dark nest over the acceptable but less preferable bright nest. This shows that the colonies are not 'satisficing'. If they had have been then the colonies would not have differentiated between the lower values for each attribute and the higher values, as they are all above a threshold of acceptability. So they are using one of the more computationally expensive strategies. A question related to this is what is the relative importance or weight given to each variable that the ants consider important in a new nest. To answer this I would need each variable to have both an acceptable value and a preferable value. This is to ensure that I am offering the colonies a non-trivial choice. Both of the above variables qualify, as does nest entrance width, so I tested to see what was the relative importance of each of these variables to a colony.

First, the colonies had the choice between a dark nest with a height of 0.8mm and a bright nest 1.6mm tall. Thirteen out of sixteen colonies chose the darker nest ($p = 0.0032$). Darkness is more important to the ants than headroom. Then I offered them the choice between a 1.6mm high nest with a 4mm wide entrance and a 0.8mm high nest with a 2mm entrance width. Twelve out of thirteen colonies choose the taller nest ($p = 0.0016$). Therefore, height of a nest is more important to colonies than is nest entrance width.

2.3 Discussion

Leptothorax albipennis colonies have a very precise lower limit for the area of a nest into which they will move. At colony sizes tested, colony size does not have an effect on this area choice. Also important to the colonies are the cavity height of the nest, its entrance width, and the illumination of its cavity. The shapes of nests tested did not have an effect on the choices made by colonies. The brightness of a nest is more important to a colony than the nest height, which in turn is more important than nest entrance width.

The ecological significance of each of the nest variables, discovered to be important to the ants in this artificial context, has yet to be tested. Nevertheless, it is easy to imagine why each of them could be important. The number of ants a nest can hold is directly proportional to the area of the nest. Franks et al. (1992) showed that these ants allow themselves $5mm^2$ per ant when building internal walls. The smaller cavities might not be able to contain the whole colony or allow for its future growth. This is vitality important and it can be seen why the colonies have such a precise lower limit.

The lack of a discovered upper size limit is probably more to do with the practicalities of my experiments than with the colonies' preferences. However, it is likely that the colonies are less choosy about an upper size limit, especially if the nest has only a single small entrance. *Leptothorax albipennis* can build internal walls to reduce the cavity if it needs to. However, as a theoretical limit, when would a nest become large enough to stop appearing to scout ants as a nest? When would they treat it as just an open space?

The other interesting result to do with area is that the size of the colony does not affect the choice of the size of the nest. This could be because the variance in the size of the colonies was not great enough for a statistically significant result to show itself. However, it is possible in the wild that the colonies do not come any bigger or smaller than those used in this experiment (Partridge et al. 1997). The two sizes of the nests were perhaps indistinguishable for the colonies. The small

nest is smaller than the previously rejected five eighths nest. Perhaps, all viable colonies would find the small nest too small.

It may be that this is not the right experiment to test for colony size effects. If the colonies were offered a larger choice of nests with subtler size differences between the nests, perhaps an effect would be noticed. This experiment would have a lot of practical complications. The larger number of nests would require a much bigger arena. With more than a small number of nests, the positions of the nests would become vitally important. For many of the new potential nests the colony could not be placed symmetrically between them. The best way to compensate for that would be to have a large circular arena with a small opening in the centre of its base through which the ants can enter the arena. The ants' old nest would be in a separate chamber underneath the arena.

When the colony occupies a nest with a cavity height of 0.8mm, the ants are restricted when manipulating brood (personal observation). This nest height is used in the lab at Bath because it forces the ants to live in an almost two-dimensional environment that is excellent for filming but is a stop to social hygiene etc. This might be why the colonies prefer the 1.6mm height nest. The 2.4mm height nest could have been rejected because its height interferes with thermoregulation or other facets of a colony's homeostasis. It may also allow larger competitors/predators into the nest. Nest sites are often a limiting resource for ants (Herbers 1986; Foitzik and Heinze 1998).

Relating to the last point about predators/competitors, the wider the nest entrance, the larger is the colony's effective defence perimeter, it is not surprising therefore that ants choose the thinnest nest entrance offered to them. If the colonies are given any building material they will use it to reduce the nest opening still further. There are probably competing pressures, just are there are for nest cavity height, for nest entrance width. A pressure to reduce the entrance width to prevent unwanted guests and a minimum width that is necessary to allow a nestmate carrying food or other nestmates to enter.

It was possible that the colonies used in these experiments were accustomed to a particular shape of nest. The results of the shape choice show that this is probably not the case. Shape should only be important if it somehow reduced the efficiency of the colony. Social organisation could be disturbed, by perhaps reducing the contact rates between nestmates. The ability of the colony to regulate its environment could also be effected by nest shape; a nest shape made up of several compartments could lead to a build up of waste products etc.

Numerous studies have looked at what attributes of a potential new nest site are considered by a swarm of house hunting honeybees (Lindaeur 1955; Lindaeur 1961; Seeley 1977; Seeley and Morse 1978; Seeley and Buhrman 1999). They include; protection from wind and sun, dryness, freedom from ants, distance from the parent colony, nest volume, entrance size, and presence of combs from an earlier colony. Seeley & Buhrman (1999) claimed that the honeybee swarms are using a 'weighted additive' strategy to decide between potential sites. The honeybee swarm would show a powerful computational ability in using this most sophisticated of decision-making strategies. However whether the swarms are in fact using this strategy is far from clear. No work has been done yet on the weights that are given to the various attributes by the honeybee. At the very least then it is also possible that the swarms are using an equal weight heuristic.

Nest site selection whether for bees or ants is similar, but not identical to the mate-choice problem that has already attracted much attention from behavioural ecologists (see Bateson (1983) and Ryan (1997) for review). The actual criteria used by females to choose mates will of course be species specific. These criteria have been reviewed several times (Trivers 1972; Halliday 1978; Wittenberger 1981; Valone et al. 1996). Examples of criteria include; correct species, male readiness to mate, male mated status, health of male, age of male, persistence in courtship and aggression during courtship. Wittenberger (1983) discussed the possible decision making strategies ("tactics") that are open to females. He considered the satisficing heuristic ("threshold criterion'), elimination by aspects

heuristic ("Priority system") and the weighted additive strategy ("gestalt criterion"). He discussed these options in the abstract as due to the experimental difficulty no one has attempted to qualify which decision-making strategy is being used in any particular case.

What about the decision-making strategy being used by *Leptothorax albipennis* colonies. They are not using a satisficing heuristic to decide between nests (see results). For identical reasons they could not be using the 'elimination by aspects' heuristic. The important point about this heuristic is that it involves elimination of alternatives until only one is left based on whether the value for the particular attribute reaches a cut-off point or not. The most important attribute I found was brightness of the cavity. If an 'elimination by aspects' heuristic was being used, 'light' (uncovered) would be the cut off point (colonies move in to it), and the colonies would show no preference for the otherwise identical covered nests. As the results show they do prefer covered nests, the elimination by aspects heuristic can be ruled out.

The colonies are not using the 'equal weight' heuristic as they give more importance to the level of light in the nest, than they do to the nest cavity height. This leaves the 'weighted additive' strategy or the lexicographic heuristic. When I began designing experiments to elucidate which of these two it was, I quickly came to a problem. If the colonies were using a 'weighted additive' strategy and the weight of one attribute was greater than the combined weights of all the other attributes, this situation would be experimentally indistinguishable from the lexicographic strategy.

Many reactions here would be 'if it sounds like a cow and looks like a cow, then it is a cow'. That is, if these two strategies are indistinguishable to the observer then there is no functional difference. However, I am interested in the computational ability of an ant colony, so even if the result is the same, it matters to me which strategy is being used by the ants. If I am to get around this obstacle, I need to ruin a surprise a little. In chapter 5, one of the discoveries I make is that it is not

necessary for all individual scout ants to compare all nests for a collective decision to be made. In the lexicographic heuristic, it is necessary that the alternatives be directly compared for the currently examined attribute. The chapter 5 result shows that the ants do not have to do this, rather the majority of ants report back to the colony with a single abstract measure of the quality of the nest.. Seeley and Burham (1999) do not mention the possibility that the honeybees could be using a lexicographic heuristic. However, just as with *Leptothorax*, honeybee scouts do not need to compare both nests. Therefore, implicitly, the lexicographic strategy can be ruled out in this case as well. All the evidence so far concurs with the hypothesis that *Leptothorax albipennis* colonies use the most sophisticated and computationally expensive decision-making strategy to decide between potential new nests.

The relative weights of the different attributes are beginning to be discovered. Brightness of the nest is more important to colonies than nest cavity height which in turn is more important than nest entrance width. Future work will catalogue other attributes and their relative weightings. A possible research avenue could be to actually test in the lab the fitness effects of different alternatives for each attribute. It can be expected that natural selection has shaped the colony's decision-making process in such a way that the resultant behaviour sequences are optimally adapted to the current environment. If there are fitness effects due to nest quality, then colonies housed in different nests should on average have different productivity (measured as an increase in the live weight of a colony). If the fitness effects equated to the weights for each attribute, this would be very satisfying.

However, findings from this approach could not be seen as a test of which decision-making strategy the colonies are using. It is possible that some feature of the decision-making process is unable to code some attributes in a way that corresponds to the fitness effect of that attribute. Imagine if a large amount of light entering a nest interfered with area assessment of that nest, by overloading

the ant with stimuli. Perhaps darkness or light has none or little effect on the productivity of the colony. Then 'cover' would have a weighting that was disproportionate to its actual fitness effect. Or imagine if the fitness effect due to darkness was to avoid being out in the open. Microscope slides are a rare occurrence in the wild. The fitness effect due to avoiding open spaces (liking dark nests) would not appear in the laboratory, but its large weighting value could still be recorded.

An animal's decision-making ability is controlled by two variables. The first is the structure of the task environments and the second is the animal's computational capabilities (Simon 1990). Daily living is a risky business. For example, if an animal is in danger of being eaten or starving to death, while deciding, this will reduce the amount of time and hence thoroughness of the decision. This is an example of a task structure limitation. Swarms of honeybees can spend several days 'debating' the different alternatives before deciding on one particular nest site. *Leptothorax albipennis* colonies often take little more than an hour. A swarm of thousands of stinging bees can afford to be tardy on their deliberations compared to the near defenceless hundred or so ants that makes up a *Leptothorax* colony. Yet, it seems likely that ant colonies are just as thorough in their decision making as honeybees.

As an example of a computational capacity limitation, the weighted additive strategy requires that the animal deciding can remember the different alternatives, whereas the satisficing strategy requires no such memory. Both the honeybee swarm and the ant colony may use the weighted additive strategy, but the individual scout does not have to remember all the nest sites so that she can individually compare them. She must only remember the one she visits, individual scouts do not have to compare different nest sites. The 'memory' capability is encoded in the information centre function of the swarm or colony (Seeley 1985b).

So far the computational effort of the different decision-making strategies has been compared only relatively. For example, the weighted additive strategy requires more computational effort than the satisficing heuristic. Attempts have been made by psychologists to create a scale of 'mental effort'. Newell and Simon (1972) have suggested that cognitive processing effort can be measured in terms of the number of 'Elementary Information Processes' (EIPs) it takes to complete a task. An EIP could include such mental operations as reading a piece of information into short term memory, comparing the values of two alternatives on an attribute to determine which is larger, and multiplying an attribute value by its respective weight.

Bettman et al. (1990) used the following set of EIPs to quantify the computational effort required in decision-making. (1) READ an alternative's value on an attribute into short-term memory. (2) COMPARE two alternatives on each attribute. (3) Calculate the size of the DIFFERENCE of two alternatives for an attribute. (4) ADD the values of an attribute. (5) Weight one value by another (PRODUCT). (6) ELIMINATE an alternative or attribute from consideration. (7) CHOOSE preferred alternative and end process.

A decision process that involved each of these steps once would have an EIP value of seven. No matter what the strategy, as the amount of alternatives increases so does the EIP value of that decision. The list of attributes that I have discovered is important to *Leptothorax* is by no means exhaustive. Nevertheless a partial EIP value can be calculated for the nest choice decision offered to the colonies. I have found 4 attributes to be important to the colonies. Therefore each scout ant must perform 4 READs, 4 PRODUCTs and 1 ADD for each nest it assesses, a total of 9 EIPs. Ants that individually compare nests must repeat this for each nest they examine and also COMPARE and CHOOSE. For the distributed process (individual comparison is not used, the majority of decisions), other ants will carry out this assessment for the other nests. The colony must then somehow (Chapter 5) COMPARE and CHOOSE. This is a total of twenty

EIPs for two nests. But importantly, this cognitive effort will be distributed across the colony. As more variables are discovered to be important to ants, this value will increase. It would also be higher in the wild were the colonies could possibly have a much higher number of alternatives to choose from.

I believe there is strong evidence to suggest that *L. albipennis* are using one of the most computationally expensive of decision-making strategies. However, which exact one is far from clear. It could be that the colonies are not using a pure weighted additive strategy. Certain (undiscovered) attributes may just have to reach a threshold. I think this is likely for attributes that make up the 'essence of nestness'. Having a roof, for example, could just be a matter of yes or no. These 'mixed strategies are well known in consumer choice models (Payne *et al.* 1993).

Another area of contention could be as to whether the effects of attributes are, in fact, additive or not. My experiments do not exclude the possibility that these effects are interactive with each other. Perhaps having a large surface area decreases the importance of having a high enough cavity. Future experiments could test this for each attribute quite easily, but not until all possible attributes have been discovered and examined in this way, could it be said for sure that the colonies use an additive strategy.

The final concern is one of context. In the Introduction, I mentioned how vitally important context factors are to the decision making process. What if the mediocre value for cover (brightness) is actually a much more sub-optimal nest than the mediocre value for cavity height (0.8mm) is. Then my experiments could be distorting the weights given to the various attributes (the effect proscribed to an attribute is its weight by its value). The way around this is to give the colonies the choice of many subtly different values for each attribute and repeat this choice many times. The results of this experiment would give us a measure of how desirable each value of each attribute was to the colonies. The weight comparison experiments could then be repeated with these now rigorously tested superior (optimal) and mediocre (least sub-optimal) values. Although, this

knowledge is important, the key point about using decision-making as a test of cognitive abilities is not what the actual weights of the nest attributes are, but rather, the integrating ability possessed by the colony. Whatever the weights are, or even if weights are equal, colonies of *L. albipennis* integrate many different attributes of a prospective nest when making a decision.

This chapter detailed experiments trying to test the computational ability of *L. albipennis* colonies. They have passed with flying colours. Although I have not elucidated fully the decision-making strategy being used by the colonies, it is clear they are using one of the most computationally expensive of these, similar, to that used possibly by honeybee swarms. But and importantly, they do not share anything like the resources of a honeybee swarm. They are much more at risk while making a decision. They do not have the same workforce for scouting or decision-making. Nor do they have the integrating power of the honeybees dance floor and waggle dance (see Chapter 5). Early in the discussion I suggest how they might be able to do this. The computational effort of using a weighted additive strategy could be spread over several ants. Chapter 5 will discuss the mechanics of how the colony is able to make such decisions despite their limitations.

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Chapter 3

INDIVIDUAL-SPECIFIC PHEROMONES

The ant has made himself illustrious
Through constant industry industrious
So what?
Would you be calm and placid
If you were full of formic acid?

Ogden Nash

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3.1 Introduction

Since 1670 when formic acid was isolated from a distillate of *Formica* workers, chemical production and communication has been linked closely with ants in the general imagination as the doggerel on the title page shows. It would seem petty to point out that the simplest of the organic acids is only found in the subfamily Formicinae (Hölldobler and Wilson 1990), as it is true that chemicals play a central role in the organisation of an ant colony. In this chapter, I will describe my investigations into the role of chemical marks in the scouting of prospective nest sites by *Leptothorax albipennis* colonies when their old nests are destroyed. As a prelude to this, I will review a small proportion of the vast amount of literature on the role of chemical communication in ants.

Pheromone is the general term used to describe chemicals involved in intraspecies communication. Hölldobler and Wilson (1990) define them as "a chemical substance or a blend of substances, usually a glandular secretion, which is used in communication within a species". In ants, they are involved in sex, trail forming, recognition, alarm behaviour and probably building behaviour (see Hölldobler and Wilson (1990) for a review.

Where and from what are pheromones produced? The archetype worker ant is loaded with exocrine glands. More than ten organs have been implicated in the production of chemicals for communication (Hölldobler and Wilson 1990) (see Figure 3.1). Classification of pheromones by chemical structure reveals that many naturally occurring compounds (such as host odours) and pre-existing metabolites (such as cuticular waxes) have been coopted by ants to serve in the

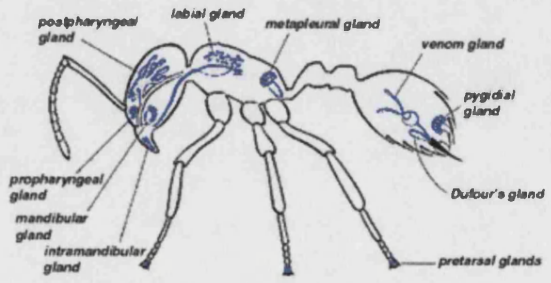

Figure 3.1 Generalised exocrine system of an ant

biochemical synthesis of their pheromones (Gullan and Cranston 2000). The pheromones produced form a bewildering catalogue of organic chemicals: aliphatic hydrocarbons, alcohols, ketones, esters, acids, lactones, organic sulphides, pyrazines, ethyl ketones, and phenols.

Pheromones can have one of two general classes of effects. *Primer* effects are those substances, which alter physiologically exocrine and reproductive systems, thus preparing the body for new biological activity. An example of this type of effect can be seen in the migratory locust (*Locusta migratoria*). When populations of this insect are low, locusts develop into the solitary phase, with a uniform-coloured nymph and large sized adult with large hind femora. At high densities, a dark stripped nymph develops into a smaller locust with shorter hind femora (gregarious-phase individual). The most conspicuous difference is in the behaviour of each phase type. Solitary-phase individuals shun each other's company but make concerted nocturnal migratory movements that result eventually in aggregations in one or a few places of the gregarious-phase individuals, which form enormous and mobile swarms. This behaviour shift is entirely due to the crowding levels, one of the most important cues of which is the pheromone (odour) of other locusts (Gullan and Cranston 2000).

The other class of effects that pheromones can have is *releaser* effects. Here the pheromone induces (releases) a specific behaviour response (Wilson 1958). When an *Acanthomyops claviger* worker is attacked, she reacts by discharging the contents of her Dufour's and mandibular glands. When other workers sense this volatile cocktail they display the following response: the antennae are raised, extended, and swept in an exploratory fashion through the air; the mandibles are opened; and the ants begin to walk, then run, in the general direction of the disturbance (Regnier and Wilson 1968)

Who the message, encoded in the pheromone, is meant for is very important in the design of the chemical substance. Should it be anonymous and non-specific or would it be useful if only the ant that laid the trail could sense it or recognise it

amongst other signals. A signal could be species specific, colony specific or individual specific or any other functional subgroup that could be imagined. To understand how the level of 'privacy' of a pheromone (Hölldobler and Carlin 1987) could be altered, pheromone blends must be considered.

Pheromone blends are combinations of pheromones from different exocrine glands that work together to produce a signal. Hefetz (1990) proposed that they evolved mainly because a multicomponent signal with a fixed composition is a much clearer signal in an already highly odourous environment. An example is the alarm response of *Acanthomyops claviger*. The highly modified poison gland, typical of the Formicinae, appears to produce only formic acid, used in defence. But the multiple terpenoid aldehydes and alcohols of the enlarged mandibular glands serve in both defence and alarm. Among the homologous alkanes and ketones of the Dufour's gland, undercane is an alarm pheromone, whereas the remaining components serve mostly in defence.

Leafcutter ants use different blends of trail substances to ensure species specific privacy of the signal. Species of *Atta* and *Acromyrmex* either react to or produce in their poison gland the pyrrole methyl 4-methylpyrrole-2-carboxylate. Yet, *Acromyrmex octospinosus* actively avoids trails of *Atta cephalotes*, an effect that is due to components that occur in blends with the pyrrole (Blum 1982).

The solitary bee *Eucera palestinae* nests in aggregations. It marks its nest entrance with a secretion from its Dufour's gland (Shimron et al. 1985). Smearing a nest entrance with this secretion from a non-self bee causes the nest owner to hesitate entering the nest. No other parts of a non-self bee have this effect. The nest marking secretion is individual specific. Another example of an individual specific marker is found in the aphid parasitoid wasp *Praon pequdorum* (Danyk 1993). This wasp can recognise aphids that she has already laid eggs in. This recognition is due to a pheromone secreted by the wasp.

The perception of a simple stimulus is due to a particular sensory receptor firing. The perception of complex pheromone blends could involve many sensory receptor types, each sensitive to different ranges of constituents (O'Connell 1975). O'Connell (1975) proposed that the specificity of pheromone blends is encoded in the insect brain by the overall pattern of receptor firing. If a series of similar, but not identical, blends evokes the same pattern in the sensory receptor neurons or the central nervous systems, where receptor firing patterns are integrated, this series will not be perceived differently by the ant.

How could specificity evolve? The pheromones sent out by ants will not all be identical, whether because of genetic or environmental (different food sources etc.) differences. This variation may be perceptible to the receiver's sensory system, but there may be no difference in response. If there was an adaptive advantage to reacting differently to different variants, selection will favour individuals that are able to do so.

The present study details experiments carried out to begin to analyse the assessment procedure of scouting *L. albipennis* ants. Initial results suggest the involvement of chemical marks. These are considered with reference to their specificity.

3.2 Methods

3.2.1 Marking of colonies

Sixteen colonies of *Leptothorax albipennis* (Curtis) were collected from Portland Bill, England, in April and June 1998. I marked each ant uniquely with three tiny paint marks, of various colours, on their gasters (Sendova-Franks and Franks 1993). For the purpose of these experiments it was only necessary that those ants which investigated a new nest retained their paint marks.

3.2.2 Video recordings of normal nest prospecting

Five emigrations were performed: one per colony. An empty nest was placed 10cm away from an occupied nest that had been removed from its housing petri dish and placed in a large petri dish (220mm x 220mm x17mm). This large petri dish was thoroughly cleaned with ethanol prior to each emigration.

A video camera was focused on the new nest to record all the comings and goings of the ants. Because of the poor colour depth which S-VHS videotape affords, I needed to record manually which ants were entering and leaving the new nest site. As the ant entered its colours were dictated into a microphone and recorded on the audio channel of the videotape. Using the videotape, I could therefore identify each ant as it entered and left the new nest. Also recorded were the length of time that each ant spent in the new nest and the behaviour of the ant during such visits.

3.2.3 Nest substitution experiments

The experimental arena consisted of a large petri dish. Placed into this were the housing petri dish with the colony and a 'target nest site' i.e. a new nest (various designs, see results) with a plastic antechamber. This plastic antechamber was used to deny the ants access to all but the very front of the nest entrance and the whole of the nest cavity. Joining these two structures was a plastic bridge, 130mm long and 10mm wide (see figure 3.2). This bridge was cleaned with ethanol before each new emigration. The recording set-up was the same as that used during the video recording of the normal emigration experiments. Only one ant at a time

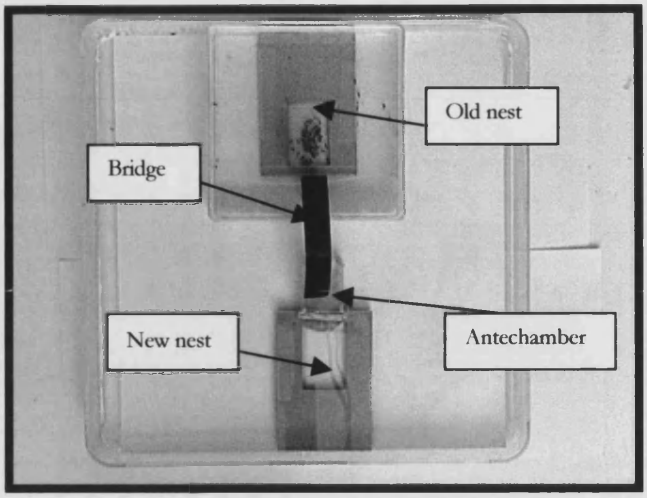

Figure 3.2. Experimental set-up used during bridge experiments. A video camera was placed above this equipment

was allowed to inspect the nest. Other ants were prevented from using the bridge if an ant was already in the nest.

3.3 Results

3.3.1 Video recording of normal emigrations

The aim of this experiment was to examine the normal scouting behaviour of the ants. The median time spent in the new nest per ant per visit for all visits was 80 seconds (Median +/- Interquartile range = 80 +/- 123, N= 202). During a visit to a new nest site a prospecting worker, typically spends almost all of her time, in the nest cavity, walking on the floor area. One third of all the ants that visited the nest did so only once (16 from 48 visits). Of ants, that recruited nest mates to the new nest, 72% made repeated visits before beginning such recruitment (13 out of 18). Among ants that made repeat visits to the nests, three was the modal number of visits (Figure 3.3). The actual movement patterns of the scouting ants will be investigated in the next chapter.

Is there a trend, over successive visits, in the length of time that an individual spent in the nest? As three was the modal number of repeat visits, data from ants that visited the nest three times were used. These durations were not normally

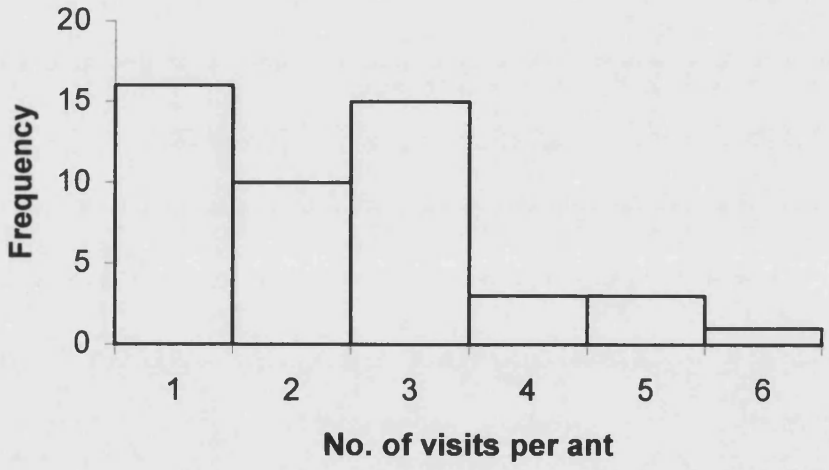

Figure 3.3. Histogram shows the distribution of number of visits per ant. Three is the modal number of repeat visits to the nest by one ant.

distributed so Friedman's two-way analysis of variance by ranks was used. The three ranks used were; the longest visit, the intermediate visit and the shortest visit. Ants were most likely to spend the longest time in the nest on their first visit and each subsequent visit was shorter than its predecessor ($\chi^2_{r2} = 6.14$, $p < 0.05$) (Figure 3.4).

3.3.2 Nest substitution experiments

How can the decreasing length of time spent in the nest on each ensuing visit be explained? How does the ant know it has visited the nest before? One possible explanation is that the ant remembers where it has been or it remembers some visual or other pre-existing physical cue about the nest cavity or the surrounding area. To examine this, I did the following: after an identified ant had entered the target nest site and returned over the bridge to the old nest, I substituted the visited nest with a previously unvisited 'clean' nest. Only the previously identified ant was allowed to return over the bridge to prospect this nest. Again after the ant's second visit, this second nest was replaced. Then for a third and final time the ant was allowed to return to the new nest site.

The scouts who encountered this nest type did not show the decreasing trend in successive visit length, as displayed in standard nest prospecting, see figure 3.4 ($\chi^2_{r2} = 0.3$, NS). So although all of the nests used were made to the same specifications from the same materials and, after the swap, the replacement nest was placed in the same position which the original nest had occupied, the ants did not realise that they had visited the nest before. Therefore a scout is not using some pre-existing cue to remember that it has been to the nest before.

So how does the ant know that it has visited a nest before? The most parsimonious explanation is that the scout is chemically marking the nest to alert it to the fact it has previously visited the nest. If an ant were leaving some sort of

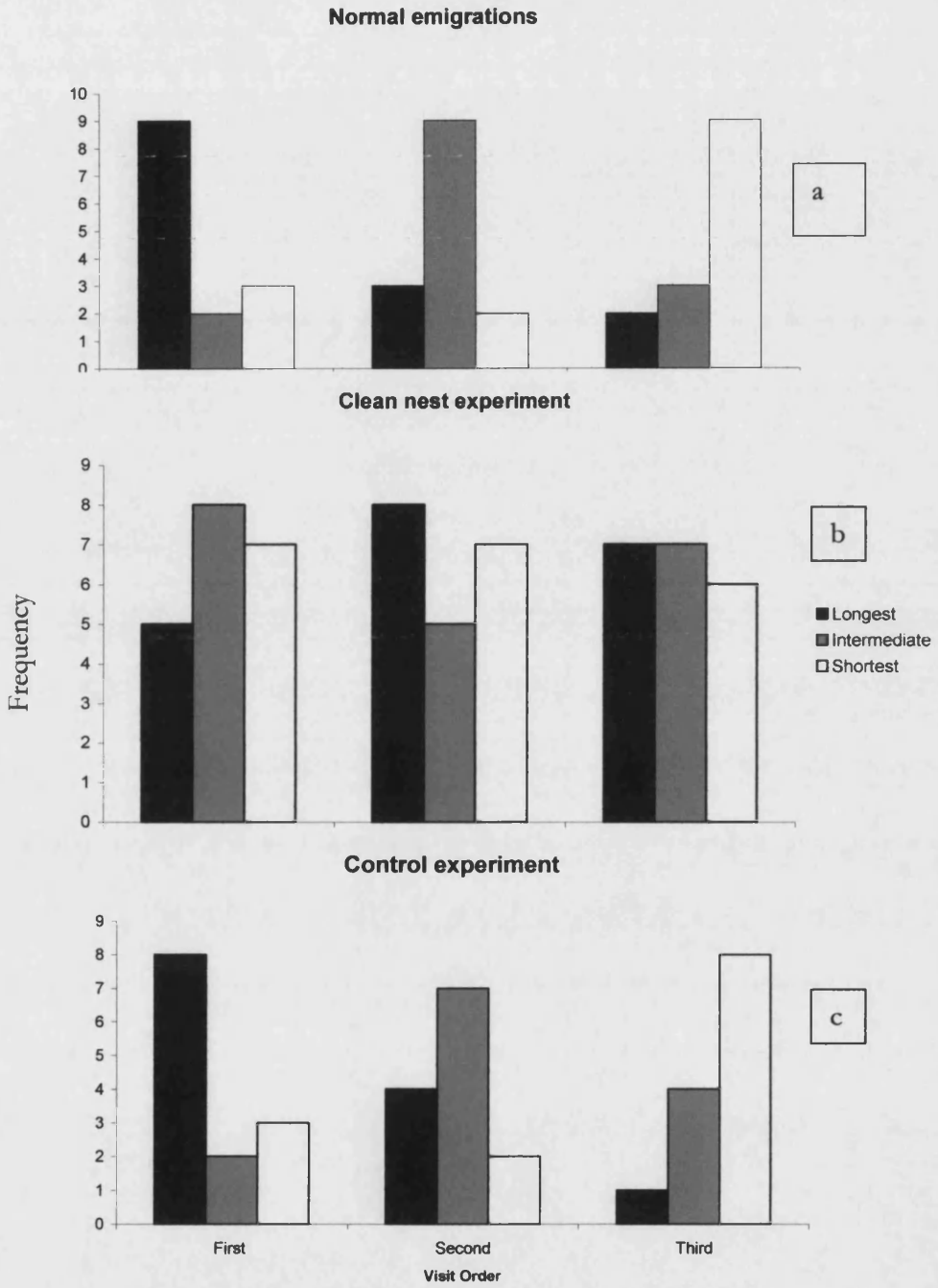

Figure 3.4. Distribution of ranks of visit length during (a) normal prospecting, (b) clean nest substitution experiments, (c) control experiment. During normal prospecting one rank of visit length dominates on each visit. During the clean nest substitution experiment ants spent the same amount of time in the nest on each of their three visits. The control data show a very similar trend to the normal emigrations

chemical mark, this would explain the result from the clean nest experiment. If an ant left a mark, this mark would have disappeared when we replaced the nest. The ant therefore would treat the otherwise indistinguishable nest as a new nest and begin the assessment routine all over again.

A problem that could be foreseen with chemical marks inside the nest is that other ants are both concurrently and consecutively examining the same nest and therefore possibly also laying pheromones. This is a problem involving the privacy of pheromones (Hölldobler and Wilson 1986). It might be useful if each ant had a unique mark that it could detect among the throng of other marks that it would encounter. In such situations selection may favour individual specific pheromones.

This issue of pheromone specificity prompted the final two experiments. It is possible that the trail pheromone(s) are the same among colonies of the same species. An identified worker was allowed to enter the target nest site and return over the bridge. But instead of a clean nest being substituted, a nest that had been recently examined by ants from a different colony was used. The length of time, between when the foreign worker left the nest and when the identified worker was allowed to examine it, was similar to the average length of time between an individual ant's successive visits during normal nest prospecting.

For this 'foreign colony' and the following 'same colony' nest substitution experiments it would have been difficult, due to timing problems, to examine three visits to the nest. Therefore, the foreign colony and same colony experiments had two rather than three visits each. The Wilcoxon signed ranks test was used rather than Friedman's two-way analysis of variance to test for significance. In the foreign colony substitution, there was no significant difference between the length of the first visit and the length of the second ($z = -1.224$, $N = 14$, $p = 0.221$). So the scouts either do not sense or choose to ignore marks left by other colonies.

Is the marking pheromone shared between nestmates? To test this I allowed a worker from the same colony to prospect the replacement nest before the identified ant entered it. To prepare the replacement nest, a different nest and bridge were introduced to the colony while the identified worker was prospecting the target nest site. This new bridge and nest was placed at right angles to the first. A single ant (not the identified ant) was allowed to make one scouting trip to this alternative nest. This nest then replaced the nest that the identified worker had prospected. Again there was no significant difference between the length of the first visit and the length of the second (Same colony: $z = -0.336$, $N = 16$, $p = 0.737$). The pheromones laid by each scout ant is specific to her, it is individual specific.

I performed a control to examine the influence, if any, of the physical disturbance associated with the temporary movement of the bridge and the new nest. Rather than the original prospected nest being exchanged for a different nest, the original nest was moved to the side by a distance equal to its width, and it was then returned to its former position. The data for this control showed the standard decreasing trend (Fig. 3.4) ($\chi^2_{r2} = 6.00$, $p < 0.05$). Therefore, it is unlikely that the actual protocol of the experiment influenced the results.

3.4 Discussion

Leptothorax albipennis ants that scout potential nests when their old nest is destroyed make repeat visits to these sites. While there, they mark the nest sites with a chemical. These chemical marks are ignored or not recognised by all other ants bar the individual who laid them. That is, they are individually specific.

Both (Maschwitz 1986; Aron et al. 1988) have reported that other *Leptothorax* species use individual specific trails for orientation outside the nest during foraging and nest emigrations. Recruiter ants use these trails to orientate; the trail itself does not attract recruits as it does in mass recruitment species. The group recruiting ponerine *Pachycondyla tesserinoda* also uses individual specific trails in this way (Jessen and Maschwitz 1985; Jessen and Maschwitz 1986).

No explicit trail-laying behaviours, for example sting protrusion or pressing their gasters on the substrate, were seen during the experiments described in this chapter. However this does not rule it out, as the protocol was not ideal for such an observation. I tried to record any such behaviour by using 'smoked glass' as the floor of the nest (Hangartner 1967). Maschwitz *et al.* (1986) found that *L. affinis* generated tracks in which the imprints of gastral hairs was found, implying that this species presses its gaster to the ground during trail laying. However this was in the arena, in my set up the scouting ants had to enter the nest first. All the ants that entered the smoked nest left almost immediately. It was obvious that the ants would not emigrate into this sooty environment. This made it impossible for me to gain any useful records. At the present time, it is unclear what is the trail laying mechanism used by these ants. A future experiment might smoke the entire arena and allow the colonies to get use to it as a surface and then to introduce a new smoked nest to them and record the trails.

Is it correct to call the trail left by scouts in new nest sites a pheromone trail? It is normally assumed that a signal (something refined for carrying information by natural selection) or cue (something that provides information without being specifically designed for it) requires an actor and reactor that are not the same

individual (Krebs and Dawkins 1992). In all the papers dealing with individual-specific trails, the chemicals that the trails are composed of are referred to as pheromones (Jessen and Maschwitz 1985; Jessen and Maschwitz 1986; Maschwitz 1986; Aron et al. 1988). They use it in the almost vernacular sense of 'a chemical produced by an animal'. However I feel there is value in redefining pheromone to include such individual specific messages. Why must communication (the use of a signal or cue to transmit information (Seeley 1995)) be defined as between individuals? After all, lots of people regularly leave little notes for themselves. Such notes obviously contain information, defined as a reduction in ambiguity.

Chemically, what is the individual specific pheromone(s)? Which gland is involved in its (') production? The poison or Dufour's glands are often associated with trail substances in myrmicine ants (Hölldobler and Wilson 1990). Maschwitz *et al* (1986) were unable to localise the part of the body responsible for the pheromone(s) which they found. They looked at extracts of the following: legs, sting glands and sting sclerites, recta and all gastral sclerities. I did not attempt to isolate the source of the trail substances. It is individual specific and to gain an extract from any body part would mean killing the ant. A dead ant could not be used in a behavioural assay for a response to the chemical (Hölldobler and Carlin 1987). Such context dependent responses to chemical stimuli are well known from many studies of insect olfactory mechanisms (Payne et al. 1986).

An interesting way to test for a response could be to use an electoantennogram. This technique measures the electrical response of the receptor cells of the insect's antennae to particular stimuli (Rumbo 1989). If a particular response was noted when an ant's antennae was presented with its own trail (from the nest floor), then the investigator could look for this response by presenting the antennae with extracts of the same ant's different body parts and glands. If the gland or glands were isolated, then a gas chromatograph analysis could perhaps show which chemicals and their respective levels are the source of the individual

specificity (Hölldobler and Carlin 1987). However this assumes that the specificity of the pheromone is encoded in the firing of the antennae. It is much more likely that it is the olfactory bulbs or even the mushroom body that integrates this behaviour (Gronenberg 1996). Although it is still theoretically possible to record from here, this is a much more specialised and long term project (Gronenberg 1999).

I have discovered that *L. albipennis* uses individual specific pheromones inside the nest. It is parsimonious to assume that these are the same pheromones used by *Leptothorax* for orientation during nest moving. Their use inside the nest is presumably to aid in estimating the size of the nest. In the next chapter this assumption will be looked at and several methods by which individual specific trails could be thus used will be tested.

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Chapter 4

BUFFON'S NEEDLE

Assessment of nest area

TABLE OF CONTENTS

4.1 Introduction

Leptothorax albipennis colonies can actively select a nest based on its internal size (chapter 2). The assessment of nest size in someway involves the laying of individual specific pheromones inside the nest (Chapter 3). The aim of this chapter is to find out how the scout ants measure the size of a new nest? As an introduction I will look at some of the mechanisms and strategies that animals use when they need to quantify their environment. How do animals acquire information about their environment and then process it into a mental image?

4.1.1 Rules of Thumb

The acquisition of information incurs costs in time, energy, exposure to predation, and/or lost opportunity. Without information, however, animals will be unable to assess the costs and benefits of decisions. Obtaining perfect information may be impossible. Do animals need their assessments of ecological factors to be perfect. It is possible that the cost of an infallible assessment process might outweigh any fitness benefits it gives through a reduction in estimation errors.

Animals often look at their environment through the filter of a 'rule of thumb' (Wehner 1987). A rule of thumb can be defined as 'an elementary decision rule based on local stimuli that contain relatively small amounts of information' (Hölldobler and Wilson 1990). The animal does not consider all alternatives or all the variables but rather looks at a subset of these to judge what would constitute a suitable response. Some contexts in which animals use a rule of thumb include nest building by wasps (Karsai and Penzes 2000), foragers deciding when to leave a site (Weber 1999), parents deciding how much to feed offspring (Davis 1999) or male ground squirrels deciding how long to stay with a female after copulation to reduce sperm competition (Schwagmeyer & Parker 1994).

Animal behaviours based on rules of thumb are often evoked to explain the lack of optimality in the animal's actions. Karsai and Penzes (2000) showed that the wasp *Polistes dominulus* had all the information available, it required to build an

optimal nest shape but because of the rule of thumb it used to survey its environs, it built sub-optimal ones. Of course, optimality assumes that the animal is a 'Laplacean Demon' (Gigerenzer and Goldstein 1996) with infinite time, knowledge and computational ability with which to carry out a task. Naturally, this is not the case, two constraints shape the assessment ability of an animal in any particular example: the limited computational ability of the animal and the specific requirements of the task at hand. These are the confines under which natural selection must act to match an animal to its environment.

This chapter is about a rule of thumb that I found was used by ants to measure nest size. What is already known about how animals measure physical dimensions?

4.1.2 Animal metrics

Relatively little work has been done on how animals measure dimensions. Most studies that deal with size of foraging area or territory, for example, consider how much space the animal requires to survive or prosper, rather than how it goes about judging this space (for example (Begon et al. 1990)). Also, I am interested in how animals measure space that is on a scale much larger than their own body size. Although far from trivial, how hermit crabs measure new shells (Elwood and Neil 1992) or how leafcutter ants judge how big the leaf pieces they cut are going to be (Wetterer 1991), can be related to simple fractions of body size. Below I give two examples of animals measuring larger than body size quantities, [1]the distance covered during a short journey and [2]the volume of a sphere. I chose these two examples because some excellent studies have been performed to examine them using the group closest to my heart, insects.

4.1.2.1 Distance estimation

Path integration is a method by which an organism, from its own movements, can deduce its current location relative to its starting position (Etienne et al. 1998). It is used extensively by animals when undertaking relatively short journeys. To perform path integration, an organism must be able to calculate

both the angles it has turned and the distance it has travelled. It is the latter variable I will discuss here.

Insects are very interesting organisms in which to study distance measurement, as they have very small interocular separations and therefore can not rely on stereoscopic vision (Collett and Harkness 1982). Numerous cues have been suggested to be connected with distance estimation in insects (Ronacher et al. 2000). These include [1]the time spent travelling, [2]the energy expended during travel, [3]self-induced optic flows and [4]idiothetic cues. The first cue is easy to imagine, if an animal were to travel at constant speed, then the amount of time for which it travelled would be a good indicator of the distance travelled (Maurer and Seguinot 1995).

von Frisch (1967) suggested that foraging honeybees use the amount of energy expended on their outward journey as a measure of distance. For many years, this was the dominant explanation for distance estimation in honeybees. It was thought that the bees need not be measuring their energy consumption directly, but rather using the stretch receptors in their crops to measure the decrease of nectar stored by the decreasing tension in the crop wall (Neese 1985).

Recently, however the energy hypothesis has been rejected as a valid explanation for honeybee distance estimation. A bee tries to keep its thorax at a temperature of 40°C during flight. For an ambient temperature of 20°C, only one percent of the energy needed for heating was used for actual locomotion. Due to this lack of resolution, energy consumption would be a very poor measure of distance for a bee to use (Esch 1996). Numerous experiments have come up with data invalidating the energy hypothesis. For example, Esch & Burns (1996) found that if bees have to fly to a feeder suspended at a considerable height, they underestimated the distance. The energy hypothesis would predict that the bees should overestimate the distance, due to the extra energy required to fly against gravity. Wehner (1992) rejected the energy hypothesis as an explanation for how *Cataglyphis* ants measure distance. He attached weights to the foraging ants;

thereby increasing the energy cost of any given distance, and found this did not effect their ability to judge distances.

Self-induced optic flow is the movement of images across the retina induced by movement of the organism itself. The integral of this image motion over time is a measure of distance for the animal to use. This is the present hypothesis used to explain the measure of distance in honeybees (Esch & Burns 1996; Srinivasan et al. 2000). Bees attempt to maintain a constant velocity of image flow over the retina when flying (Esch & Burns 1996). So when flying low (which may be required if the quality of visual landmarks is poor, e.g. over water), they move slower than when flying at higher altitudes (Heran and Lindauer 1963). The total angular image motion (the measure of distance used by the bee) that a bee senses when flying is unrelated to the speed at which the bee flies. The logic behind this is as follows (taken from Srinivasan et al. 2000). The bee moves forward by a small distance Δd at a speed of Vcm/s. The induced angular velocity A would depend on the distance away of the scene being viewed. However, for a particular scene A is proportional to V, therefore $A = kV$ where k is a scene dependent constant. The time Δt taken to fly Δd is naturally the distance divided by the speed, $\Delta t = \Delta d / V$. Therefore, during this time interval, the angular motion of the image on the eye would be $\alpha = A\Delta t = k\Delta d$, which depends only on the distance travelled and is independent of flight speed.

Experiments carried out by Srinivasan *et al* (2000) test explicitly whether optic flow is the centre of distance estimation in the honeybee. They trained the bees to fly through a tunnel. A 6.4 metre long by 11cm wide and 20 cm high tunnel that had a highly contrasting pattern on its inner surface fooled the bees into reporting the food source as being over two hundred metres away. This was due to the fact that the bees were abnormally close to the floor and walls. Therefore, for any given distance moved, the bee experiences a greater angular motion than would normally be expected. No work has been done yet on how much of this distance estimation is based on the ventral and/or lateral views of the bee.

Similar experiments were carried out on *Cataglyphis* ants (Ronacher and Wehner 1995). The ants were trained to walk on a perplex floor under which a pattern was moved at different speeds in the same or opposite directions to the ant. These experimental manipulations of the optic flow influenced the ants homing distances. It should be noted that in this work, it is the ventral surface that is being manipulated. Work by the same authors (Ronacher et al. 2000) found no effect by performing similar experiments with the moving patterns this time on the walls, i.e. the ants' lateral view.

An idiothetic cue is one that the ant derives from its own bodily movements. Examples of idiothetic cues would be the number of steps or wingbeats taken during a journey. This is thought to be vitally important for path integration in most animals (Etienne et al. 1998; Seguinot et al. 1998). Even ants can integrate their paths without reference to optical flow. If an ant's ventral eye surface is covered with paint, so it can no longer use optical flow as a cue, the ant is still accurate in gauging the distance it travelled. The length of an ant's step is constant for any given walking speed (Zollikofer 1994). During foraging trips *Cataglyphis* maintains a constant walking speed (Wehner and Srinivasan 1981). Therefore the distance travelled by an ant is proportional to the number of steps it takes and this type of pedometer is indeed probably what it uses to measure distance.

4.1.2.2 How big is this egg? Trichogramma minutum determines how much of a burden it can be.

All animals live in a three dimensional space. How can they measure volume? A good example of this need to measure volume comes from the parasitoid wasps.

The parasitoid wasp *Trichogramma minutum* lays her eggs within the eggs of other insect species. It needs to know the volume of the host egg, so it can judge how many of its own eggs to lay. The parasitoid lays more eggs in larger hosts (Klomp & Teerink 1962). To assess the number of eggs to be laid, a measure of the volume of the host egg must be calculated. How is a wasp to do this with out knowing the geometrical equation for the volume of a sphere? It uses a simple

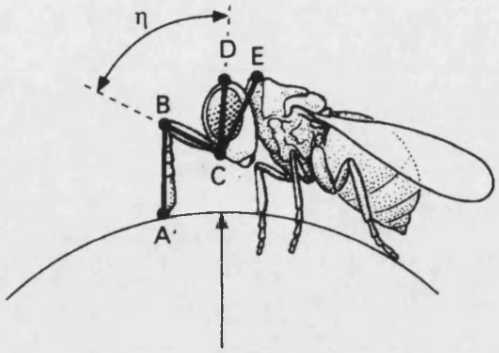


Figure 4.1 *Trichogramma minutum* measuring a host egg. Used with permission, R.Wehner

but elegant rule of thumb. If it keeps its thorax a certain height above the surface of the host egg and its thorax head angle (<DCE) constant then the scapus head angle (η) is inversely correlated to the radius of the egg and therefore the volume (Wehner 1987) (see Figure 4.1). So the wasp hasn't got an exact estimate of the egg volume, rather it has a ready reckoner for the number of eggs to lay e.g. 35 degrees =6 eggs.

4.1.3 Nest measurement

This brief introduction to animal metrics shows that if nothing else, animals do not solve these problems the way human engineers would. How do *Leptothorax albipennis* scouts measure nest area? In the last chapter I showed that the scouts were marking the new nest with an individually specific chemical. In this chapter I will describe experiments designed to elucidate how the scouts measure area and whether it involves the use of these chemical marks and/or a rule of thumb.

4.2 Methods and Results

4.2.1 Are the ants measuring area or some other lower order variable?

In chapter two I showed that the ants choose nests above a certain size. Is this decision based on area as was thus far assumed or is it some other lower order variable? Perhaps it is only length that is important or perhaps breadth is the ants sole concern. The ants were given a choice between three different nests. One that had half the standard area but the same length as the old standard nest (38mm X 11mm). One which again was half the standard area but had the same breadth as an old standard nest (20mm X 24mm). And one which was of standard area but was square in shape (side = 30 cm), so it shared neither length nor breadth with the standard nest. See figure 4.2 for a diagram of the nests used during these and other experiments discussed in this chapter. Out of thirteen colonies, one chose the 'length' nest, two the 'breadth' and ten chose the area nest (G-test = 8.197 with 2 d.f, $p < 0.05$). It is area that is important to the colonies.

4.2.2 Movement of the scouts inside the nest

In the 'normal nest emigration experiments' detailed in the last chapter, I recorded the behaviour of ants that were scouting a potential new nest. All parts of the tape containing scouting behaviour were digitised as .avi files on a computer by a 't.v. card' (ATI Video Player). These .avi files were broken down into single images (.bmp files) using a freeware program ('VideoSnap' http://www.c3sys.demon.co.uk). In this way the movement of the ants could be analysed at a rate of five frames a second. The x,y co-ordinates of the scout ant's head and gaster was recorded each frame using a program I wrote in VisualBasic. Figure 4.3 shows a typical trail of an ant on its first visit to a new nest.

4.2.3 Alternative algorithms

4.2.3-1 Internal perimeter

The first thing that strikes most people when they see Figure 4.3 is how much time the ant seems to spend going round the edge of the nest cavity (collimating activity). It is possible that the ants are using internal perimeter, measured by

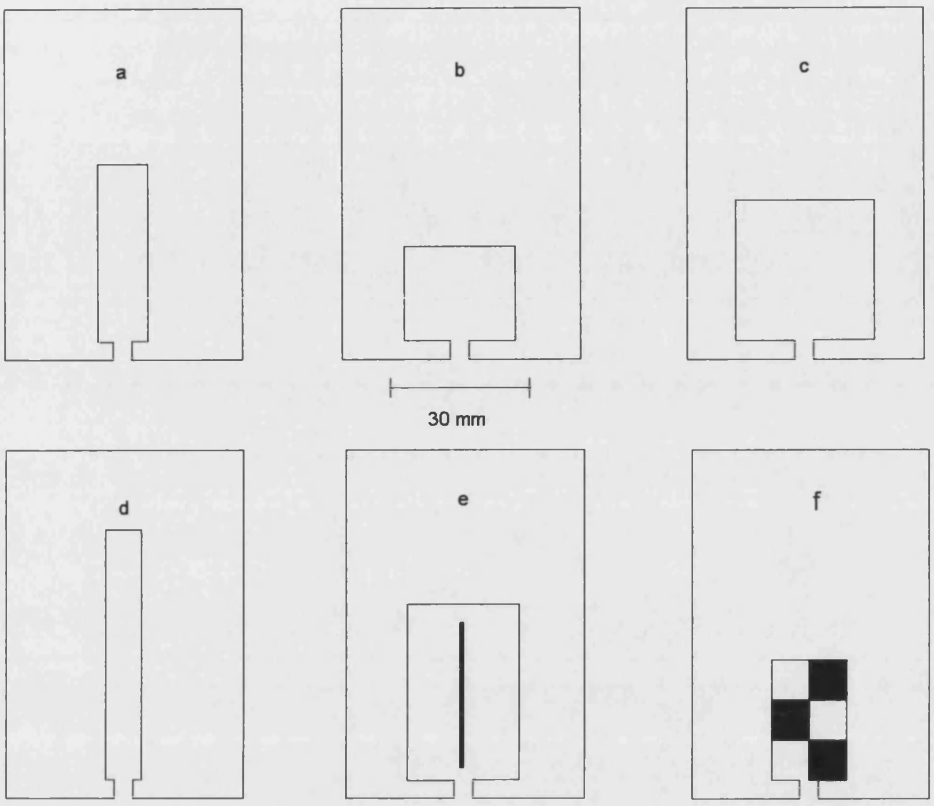


Figure 4.2 Nest Designs: (a) half standard-size nest but with standard length, (b) half-size nest but with standard breadth, (c) standard sized nest, square, (d) half-size nest with same internal perimeter as a standard-size nest, (e) standard-size partial-barrier nest - the black line is a cardboard wall from floor to roof that could be circumnavigated only at its ends, and (f) half-size magic carpet nest - the shaded areas represent the holes in the upper carpet – see text. For the other nest designs see chapter 2.

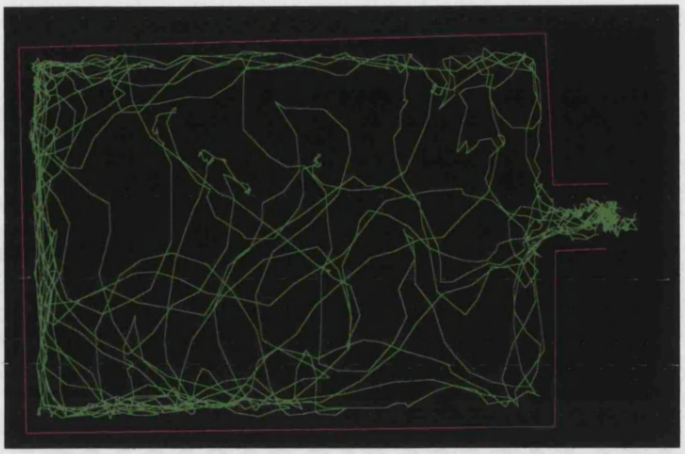


Figure 4.3 The path of a single ant during its first visit to a prospective nest. The green line is the path of the ant. The red line represents the internal nest walls.

idiothetic cues, as a crude indicator of nest area. This would not be a very reliable measure, as the more invaginated or irregular the walls were; the larger would seem the nest. However, it is possible that it is good enough for the ants' needs. Perhaps all cracks in rocks have similar levels of irregularity (fractal dimension?) and therefore are comparable using this method.

To test whether the ants are using internal perimeter, I gave the colonies a choice between an old standard size nest and a half-old standard size nest with the same internal-perimeter length as an 'old standard' nest (8mm X 54mm). If the colonies were using internal perimeter, it would be expected that they would show no preference between the two nests, after all they have the same internal perimeter. Out of thirteen colonies, ten choose the 'old standard' nest (binomial test: $p = 0.035$).

It is possible that it is the elongated shape that the colonies find objectionable, perhaps they have just become accustomed to the 'old standard' shape. To examine this I offered the colonies the choice between an 'old standard' nest and a second nest with a standard area but with a length: width ratio that is the same as the 'internal perimeter' nest (12mm X 78mm). If the colonies object to the elongated shape they should reject the 'elongated standard' nests. Out of fifteen colonies, ten colonies chose the 'old standard' nest (binomial test: $p = 0.092$). The

'elongation' of the length: breadth ratios does not effect the colonies. Therefore overall the colonies are not using internal perimeter as an estimator of nest area. The observed collimating activity may reflect a need to check that the wall is not breached in too many places and/or may help scouts return to the nest entrance.

4.2.3-2 Mean Free Path Length

Imagine a particle moving at random around an enclosed plane. The number of times the particle hit an edge would, on average, be inversely proportional to the area of the nest. Prosser (1986) simulated this behaviour and found that the average distance between collisions, the mean free path length, is a good predictor of the plane's area. The area estimation did not rely on the shape of the plane as long as the angle of incidence of a collision was unrelated to its angle of reflection.

Looking again at figure 4.3, is it possible that the ants are using a mean free path length algorithm to measure area? They seem to be covering enough space and there are enough wall collisions for a mean free path length algorithm to be viable. I gave the colonies a choice between two 'old standard' nests, one of which had a very thin piece of card (1mm wide X 0.8mm high) running down almost the entire length of the centre of the nest. If the ants are using a mean free path length algorithm, they should reject this nest, as the mean free path length associated with it is greatly reduced due to the presence of the thin central wall. Out of fifteen colonies, six colonies choose the 'old standard' nest compared to nine who chose the 'barrier' nest, this is not significantly different from an even choice (binomial test: $p = 0.153$). The colonies, therefore, are not using a mean free path length to estimate the area of the nest.

4.2.4 Back to the ants

So these two algorithms have been dismissed, what else could the ants be doing? In chapter 3, I showed that the scout ants are making repeat visits to the new nest. While there, they are laying an individually specific mark in the new nest. I also showed that on each visit they spend less time than on their previous visit.

Figure 4.4 shows the trail of one ant as it makes repeat visits to the same nest. It can be seen that the ant is covering the most ground on its first visit. The scouts move more slowly on their first visit ($3.36 mms^{-1}$) compared to subsequent visits ($4.06 mms^{-1}$)(Mann-Whitney U test: $U = 768230345$, $N_1 = 8681$, $N_2 = 9834$, $P < 0.00001$). The values for the subsequent visits was combined because there was no difference between them (Mann-Whitney U test: $U = 28076686$, $N_1 = 5463$, $N_2 = 4071$, $P = 0.06$) Any algorithm that is proposed must be able to explain this slowing down and the other previously mentioned observations.

The slower speed of an ant on a first visit could be explained by, amongst many other things, the ant needing to slow down to lay a trail. Assume for the moment that the ant is laying a continuous trail throughout its travels in the new nest. Then during its second visit the ant would intersect its previous trails as shown in Figure 4.5. Does this assumed trail affect the ant's behaviour on subsequent visits? Is there any evidence that the ant can recognise these intersection points with the assumed trail?

I looked at the speeds of ants during their second visits. Speeds were calculated every 0.2 seconds. The speeds the ants were travelling when they passed over intersections with their first visit trails were noted. An intersection was defined as when an ant was within one antenna's length (= 5 pixels) of its first-visit path. Ants probably slow down close to a wall either because they do not want to collide with it or they have hit it and this reduced their speed. To allow for this possibility, I analysed the ants' intersection and non-intersection speeds in two regions: (a) central (any point greater than 30 pixels, i.e. slightly greater than one body length, from a wall) and (b) edge (points less than 30 pixels from a wall).

Nine ants were examined; of these 6 showed significant changes of speed at intersections and all 6 slowed down (median non-intersection speed in the central region = 5.80 mm/s (interquartile range 10.44), median intersection speed in the

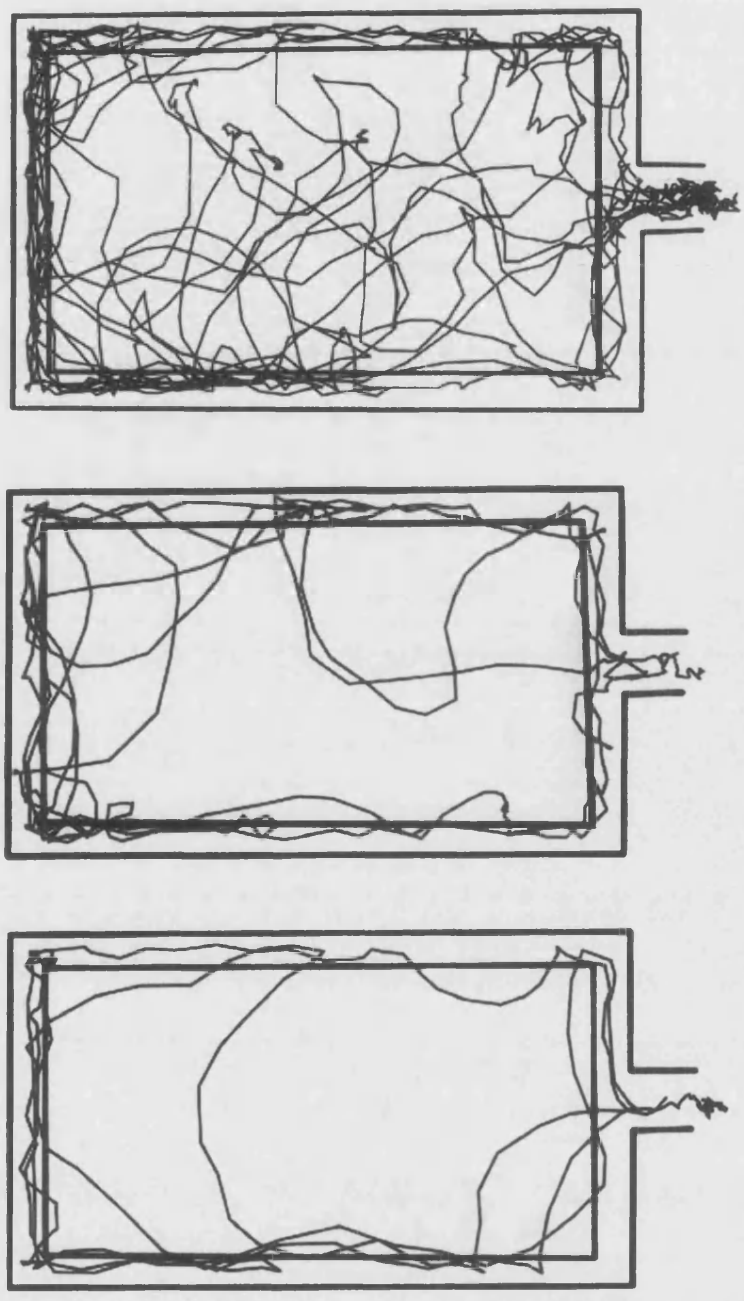


Figure 4.4 The path of a single scout (thin black line) on each of its three successive visits. The inner thick black line refers to the proscribed central region (see text).

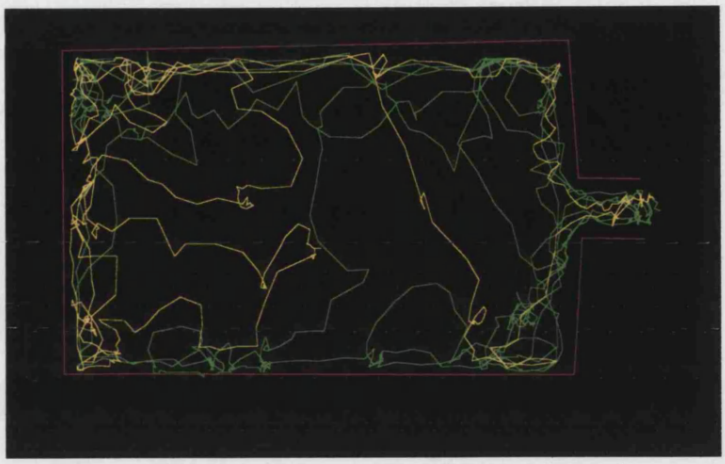


Figure 4.5 The path of ant on its second visit (yellow) superimposed on its first visit (green). The red line represents the outline of the internal walls of the nest.

central region = 3.79 mm/s (interquartile range 9.52): median non-intersection speed in the edge region = 4.53 mm/s (interquartile range 7.97): median intersection speed in the edge region = 3.04 mm/s (interquartile range 6.02)). These data were analysed using a two-way Anova design for ranks, by the Scheirer-Ray-Hare extension of the Kruskal-Wallis test (H ranged from 5.1 to 29.9; d.f. 1; p ranged from < 0.05 to < 0.001) (Sokal and Rohlf 1995). Only second visit intersections of first visit trails was examined because with third visit intersections, it was difficult to show which possible trail the ant was intersecting with; first visit or second visit.

4.2.5 Another possible algorithm: Buffon's needle.

In biology, the eighteenth century polymath, Georges Louis Leclerc, Comte de Buffon is best known for his massive Histoire naturelle (36 volumes) set out to organise all that was then known about the natural world. He was the source of important ideas about the distribution of plants and animals around the globe, relationships among species, the age of the earth, the sources of biological variation, and the possibility of evolution. The numerous illustrations to Buffon's volumes, which began publication in 1749, became, for Europeans, the source of

information about the visual appearance of creatures that inhabited every continent.

However, as the title polymath makes clear this was not the Comte's only achievement. He organised one of the first experiments to prove that lightning was electrical, basing his metallic lightning rod directly on the work of Benjamin Franklin. At the age of twenty he discovered the binomial theorem. He also worked on mechanics, geometry, probability, number theory and the differential and integral calculus.

For this chapter and how ants measure area it is his method for estimating π empirically that is of concern. This work had as its beginning the need to work out the odds of a contemporary gambling game but is seen as the beginning of the field of geometrical probability (Kendall and Moran 1963). A needle of length B dropped randomly onto a plane inscribed with parallel straight lines, I units apart (where $B < I$), has a probability $p = 2B/I\pi$ of intersecting a line (Kendall and Moran 1963). Based on such reasoning, it can be shown (Newman 1966; Franks 1982) that the estimated area of a plane ($\hat{A}$) is inversely proportional to the number of intersections (N) between two sets of lines, of total lengths (S and L), randomly scattered on to it: thus $\hat{A} = 2SL/\pi N$. This formula establishes that the number of intersections between two sets of lines could be used as a relatively simple rule of thumb to estimate area.

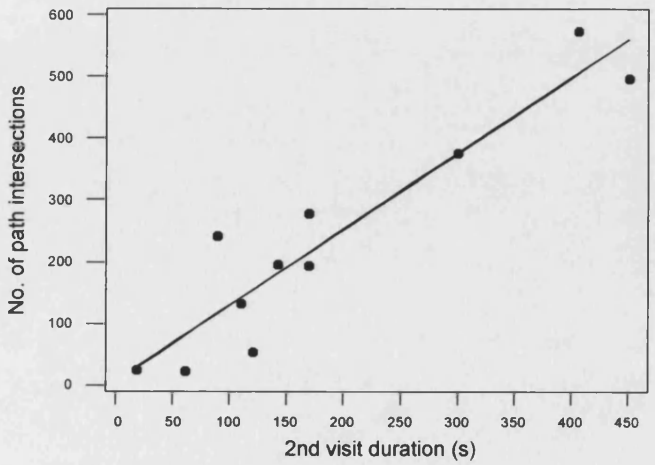
The Buffon's Needle equation for estimating area is $\hat{A} = 2SL/\pi N$. The Buffon's needle algorithm being proposed for scouts would work as follows. The scout would enter a nest, while there, it would lay an individual specific trail, the length of which is L. It then leaves and reenters the nest. Once back inside the nest, the ant walks around for a total distance of S. An ant could then estimate area $\hat{A}$ as inversely proportional to the number of intersections (N) it makes between its first visit path (length L) and its second visit path (length S). Two and π are constants and irrelevant here. It is completely equivalent if the ant is measuring

the number of intersections (N) or the rate at which it intersects its first visit path (N/S). The rate would seem the more probable measure. Animals are often assumed to have the ability to measure rate, for example, it is the cornerstone of optimal foraging theory (Stephens and Krebs 1986).

Buffon's needle algorithm would be simplest if the ants keep L constant and estimate the intersection rate between their first and second paths (see later). The duration/path length of the second visit could vary. This could influence the variance of the estimate, but not the mean intersection rate (see Figure 4.6). The duration of first visits has a distinct peak at 200 seconds (see Figure 4.7). Intriguingly, the duration of second visits also has a distinct peak at 200 seconds. If it is assumed that the distance covered by the ants during a visit is related to the time it spends in the nest, then this suggests that the ants are keeping both L and S fairly constant.

Scouts using such a "Buffon's needle algorithm" would assess nest area as inversely proportional to the rate of intersections they make between a first set of pheromone-marked paths and a second set of census paths. Hence, use of the Buffon's needle algorithm might explain why scouts make more than one visit to a potential nest site. The Buffon's needle algorithm requires the deployment of

Figure 4.6 The number of intersections between second visit paths and first visit paths as a function of the duration of the second visit by 11 scouts to nests of standard size. The relationship is best described by 'Number of intersections (N)' = 7.4 + 1.23 'Second visit duration in seconds' (r^2= 0.873 $p< 0.001$).



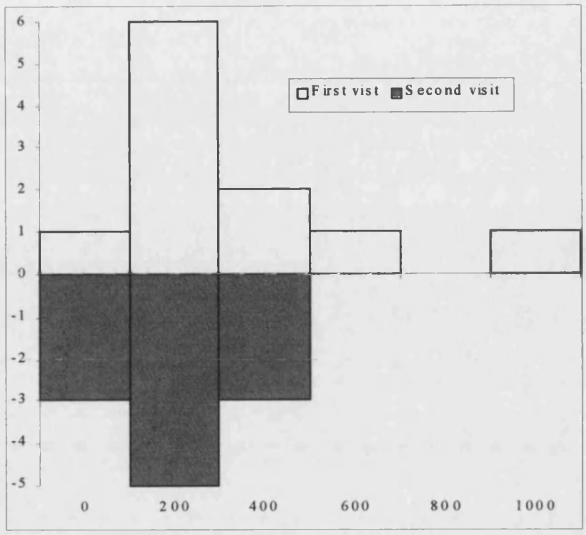


Figure 4.7 Histogram of the first and second visit durations of 11 scouts to nests of standard size.

two distinct sets of paths. Conceivably, an ant could remain within the new nest site between the deployment of its first and second paths but some transitional break between these activities is necessary. Departure from the nest would not only provide such a break but may also allow the ant to check the route between the old and the new nest. Scout ants often return to the old nest between visits to the new one.

It would also explain the need for an individual specific trail. The trail pheromones would need to be individual-specific because several scouts can simultaneously discover a potential nest site. If these ants deployed the same trail-pheromones in the new nest site the number of second-visit intersections would depend heavily not just on the nest area but on the number of scouts involved.

Buffon's needle algorithm requires that the trail pheromone is relatively long lived. Individual specific trail pheromones are likely to be more persistent than mass recruitment pheromones that can be reinforced quickly by nest mates. For example, individual specific pheromones deployed during foraging must last long enough for an individual ant to get to the end of its journey and for it to be able to retrace its steps. For *Leptothorax albipennis*, I believe that foraging distances are

likely to exceed emigration distances. Therefore, individual specific pheromones that are sufficiently long lived for foraging should be sufficiently long lived for nest assessment. Highly persistent ground-marking pheromones have been demonstrated in other contexts (Hölldobler and Wilson 1977; Hölldobler and Wilson 1986). Actually, the median inter-visit duration is only 145 seconds (inter-quartile range of 461 seconds, n = 89).

For this algorithm to be useful, the ants would have to be assessing the whole of the nest. If, for example, an ant, just by chance, spend all its time on its first visit in the top left hand corner and then on its second visit spend all its time in the bottom right corner, it would not encounter any of its trails. It would therefore think that the nest was very large. Generally, uneven distribution of trails would lead to the algorithm being highly inaccurate. The ant must be sure that its trails are sufficiently 'random'. The median number of intersections per scout between second visit paths and first visit paths in the central region and in the edge region of the nest were 178 and 172, respectively: n= 11 scouts, so there is no visible edge bias. First visit and subsequent visit paths appear to sample the whole area of the nest fairly evenly (Figure 4.4). Figure 4.6 shows the relationship between the duration of an ant's second visit and the number of intersections it makes during that visit with its first visit path. The relationship is strong and linear. This suggests that the paths are distributed to facilitate unbiased surveying. In other words, the distribution of the first set of lines (L) and the second set of lines (S) is a sufficient approximation to randomness to allow for accurate use of the Buffon's needle algorithm.

4.2.5-1 Predictions of Buffon's needle algorithm

Earlier I suggested that the easiest way of performing Buffon's needle algorithm would be to make the first visit length (L) constant. Then the algorithm would simply be that the area of the nest was inversely proportional to the rate of intersections an ant makes on its second visit with its first visit trail. Is this the

case? Do the scouts keep L constant? Is the rate of intersection inversely proportional to the area of the nest?

Sam Mugford, an undergraduate honours project student under Nigel Franks' and my supervision, performed another set of filmed emigrations. This time each colony was emigrated at different times to both a standard sized nest (35mm X 25mm X 0.8mm with a 2mm X 2mm entrance) and a twice standard sized nest (50mm X 35mm X 0.8mm). Three marked colonies were each emigrated four times, twice to a standard nest and twice to a double-standard nest. The filming protocol was as described earlier.

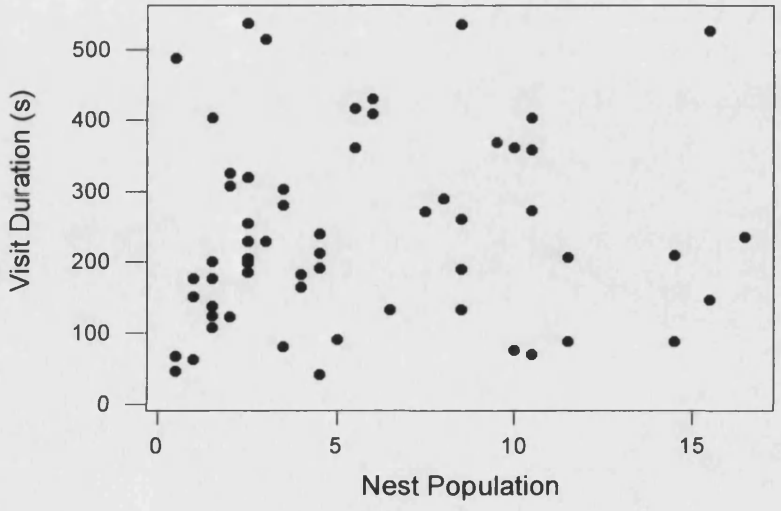
The visit distance was measured in a slightly different way from the previous filmed experiments. The paths of the visits were traced onto acetate sheets directly from the monitor by advancing the videotape at 1-second intervals and marking the position of the gaster (for first visits) or head (for second visits). For first visits we recorded gaster position, as it would indicate approximately the position of trail laying (for myrmicine ants most of the trail-laying pheromones are produced by their hind regions (Hölldobler &Wilson 1990)). The head position during second visits would indicate roughly where the ant was intersecting its first visit path with its antennae. Each point was connected to the next by a straight line and the distance measured with a map measurer. The total distance covered for each visit was recorded in millimetres. The number of intersections made between the paths of first and second visits to the same nest was estimated by overlaying the acetates from the two visits and counting the number of intersections between the two lines.

The distribution of distances travelled for each first visit of scouts from one colony (pb 8-1) was normalised by the square root transformation. There is no significant difference between the distance an ant travelled inside the nest on her first visit to a standard sized nest (raw data median: 486mm, square root transformed data: $\bar{x}$ +/- SD = 21.64+/-3.83) and the distance traveled on her first visit to a double-standard sized nest (raw data median: 600mm, square root

transformed data: $\bar{x}$ +/- SD = 25.57+/-8.43) (Paired *t* test: $t_9 = 1.79$, NS). There is also no significant difference between the visit duration (seconds) (square root transformed to normalise) of an ant on its first visit to a standard sized nest (raw data median: 222 seconds, square transformed data: $\bar{x}$ +/- SD = 15.801 +/- 4.460) and on its first visit to the double-standard sized nest (raw data median: 182 seconds, square root transformed data: $\bar{x}$ +/- SD = 13.765 +/- 4.482) (Paired *t* test: $t_{23} = 1.65$, NS). Scouts do spend the same amount of time and cover the same distance in the nest independent of the size of the nest.

We observed that when an ant enters a nest, containing several other ants, she spends time making antennal contact with, and grooming, these other ants. This might cause considerable variation in visit duration that would be unrelated to either trail laying or surveying. For example, ants that enter the new nest early in the emigration may spend less time in the nest because they do not have to groom other ants. To test whether this was the case, a correlation was performed between all first visits of ants of the colony (pb 8-1) against the average nest population of the new nest at the time of their visits. There is no significant correlation between average population and visit duration (Spearman rank correlation: $r_s = 0.168$, N = 59, P = 0.203) (see Figure 4.8)

Figure 4.8 A plot of visit duration (seconds) versus nest population at the time of the visit.



The intersection rate (intersections per mm) data was also normalised by the square root transformation. There was a significant difference between the intersection rates of an ant when it visited the standard nest ($\bar{x}$ +/- SD = 0.7193 +/- 0.2004) and the double-standard nest ($\bar{x}$ +/- SD = 0.5205 +/- 0.1660)(Paired *t* test: t_9. = 2.96. P = 0.016). For the nest sizes we looked at, the rate of intersections is inversely proportional to the area of the nest. For the standard sized nest it is just over twice (median ratio = 2.31) that of the intersection rate for double-standard nests (see figure 4.9).

4.2.5-2 An experimental test of Buffon's needle

All the findings documented above show that use of a Buffon's needle algorithm is plausible in terms of the behaviour of scouts. The key test is, however, to manipulate the ants' trail intersection frequencies in such a way that the use of a Buffon's needle algorithm would lead them to make predictable but otherwise

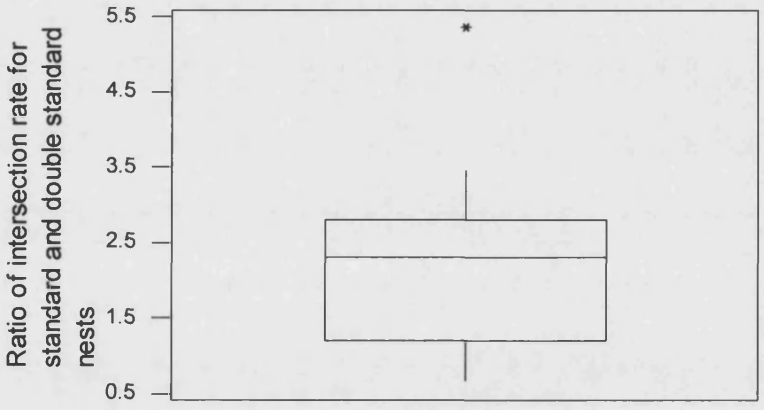


Figure 4.9 A boxplot showing the distribution of ratios of intersection rates experienced by each ant as it visits standard nests and intersection rates experienced by each ant as it visits double standard nests. The solid line inside the box represents the median of the data. The bottom and top of the box represent the 1st quartile and 3rd quartile of the data respectively. The vertical lines extending from the box represent the data inside a range of 1.5 times the interquartile range from the box. An outlier is represented by an asterix.

unexpected choices. These ants are using individual-specific trails so it is not possible for the experimenter directly to apply the trail pheromone to increase trail intersection frequencies. It is possible, however, to reduce the number of intersections. I presented emigrating colonies with a choice between 'old standard'-size nests and half-size nests. Both types of nest were carpeted with two layers of acetate sheet. The upper sheet in the half-sized nest had rectangular holes in it over half the total floor area (Figure 4.2 f). Fifteen minutes after the start of each experiment, i.e. after half the median exploration time (the time spend by the colonies exploring the nest before the first recruitment behaviour) this upper sheet in the half-size nests was removed. By removing this "magic carpet" at this time approximately half of the trails laid in the small (half-size) nest should have been removed and the number of intersections between 1st visit and subsequent paths should have been similarly reduced. As a control for disturbance the under sheet in the full-size nest was removed at the same time. In these experiments, eight out of twenty colonies chose the small nest that would normally be rejected. This is not statistically different from the colonies having no preference (binomial test: $p = 0.12$). Given that the intersection frequency in the small nest was reduced by half, an ant using the Buffon's Needle algorithm would then consider such a half-size nest to be full size. This result provides strong evidence that the ants are using Buffon's needle algorithm to measure area.

4.2.5-3 The accuracy of Buffon's needle algorithm

How accurate is this algorithm at calculating areas. For the ants used in section 4.2.5-1, the emigrations to two nest sizes, Sam and I calculated the nest area they would have perceived on the basis of their own trail laying and intersection rates. I did this by putting the empirically calculated intersection rates of each of the ten ants and their individual average first visit lengths into the equation $\hat{A} = 2SL/\pi N$. Figure 4.10 compares the mean 'perceived area' for each type of nest against its true value. I am not, of course, suggesting that ants know about π or that they calculate distances in millimetres, rather this equation is just being used to

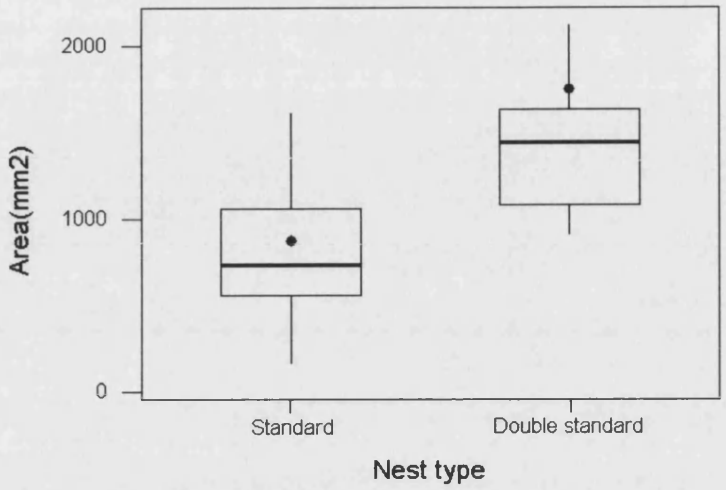


Figure 4.10 A boxplot showing the distribution of 'perceived areas' calculated for each ant on its visit to both a standard and a double standard nest. The circles represent the respective true values of the area of the two nests

calculate relative 'perceived areas' to see how much variation there is in the estimation of nest area by individual ants. Such variation is very small. It is reassuring to see how close the perceived areas are to the nests' true values. However, this is not really important. What matters is that there is a very close approximation to a 2:1 ratio for perceived areas for double sized nests vs. standard sized nests (the calculated ratio is 1.96:1). That is, ants using Buffon's needle algorithm would measure the double-standard nest as having twice the area of a standard sized nest. For other cases in which the accuracy of the rules of thumb employed by insects have been retroactively determined see, for example, (Cartwright and Collett 1983; Muller and Wehner 1988).

4.3 Discussion

In this chapter I have outlined how *Leptothorax albipennis* measures the area of a prospective new nest. This assessment is based on area not some lower order variable. The ants do not use internal perimeter as a measure of area. Neither do they use a 'mean free path length' algorithm to calculate area. Evidence in this and the previous chapter show that they are in fact using a rule of thumb that I have called the Buffon's needle algorithm.

As I said in the introduction human engineers would often not be very happy with the solutions animals use to quantify their world. However natural selection can only act on the variation present in the current population. Animals' solutions are the result of unique nervous systems with adaptive limitations, biases and distortions. Old neurons and sensory pathways must be adapted rather than replaced by new and more appropriate ones (Dumont and Robertson 1986). Animal information processing is an exercise in reducing superfluous information. Many behavioural tasks may not require elaborate representations of the external world. Often this pruning of information takes place at peripheral levels within the animal's nervous system (Wehner 1987).

Animals deal with spatial issues not by performing abstract computations performed in 3-D Newtonian space, but by adopting approximations, shortcuts and simple tricks (Wehner 1987). This can be seen in the distance and volume estimation examples presented earlier. Another excellent example of how a difficult computational problem is simplified by the use of a rule of thumb is the way male hoverflies catch females (Collett and Land 1978). When the male sees a female, he does not chase her, but immediately begins on an interception course. This calculation is much simpler if the male knows the speed and size of the female. It seems this is the case. The interception course is only successful if it is indeed a female hover fly that is being chased. The speed and size of female hoverflies appears to be hardwired into the males' brains. The computational

effort of this task has been greatly reduced by making its assessment algorithm highly specific.

If I can mention a rather prosaic and left field example, an interesting comparison of the 'human' and 'natural selection' levels (rather than the actual mechanisms) of design is a TV show called 'Scrap Heap Challenge'. The two teams of contestants are asked to build some mechanical contrivance, to carry out a particular task, out of the contents of a junkyard, e.g. build an amphibious craft that must travel one hundred metres on land and the same in water. One team is usually of a professional ilk, in the hovercraft example they were royal navy engineers, the other team are a bunch of middle age Hells Angels, for want of a better description. The Hells Angels invariably win. There are two interconnected reasons for this. First, they are used to scavenging for parts and not using the ideal tools. The second reason is that they do not over design their machines. It will do what is asked of it, but nothing else. They 'design' it very specifically with no general use in mind. The professionals on the other hand can not seem to adjust their mindset and constantly try to make the machines 'fancier' than they need be.

I would imagine that to measure the area of an irregular shape such as a nest cavity, a human engineer would use a computer to perform some sort of iterative polygon matching and measuring algorithm, e.g. the trapezoid method or the Simpson method. The trapezoid method, for example, breaks the irregular area into strips (trapezoids) that would approximate the actual shape of the nest. The area of the trapezoid is the product of its width by half the summed length of its perpendicular sides. The smaller and more numerous the trapezoids the better the fit. Integration is another solution for areas bounded by curves for which an equation can be found. A third method is to use a mechanical device called a planimeter that traces out the outline of the nest shape and mechanically integrates this to give a measure of area.

Ant colonies have none of the above tools. Instead they have come up with possibly an unique method for calculating area using the Buffon's needle algorithm. That this method is successful can not be doubted. The colonies consistently choose a (presumably) correct sized nest (Chapter 2). Animals' solutions are often unique with no general structure. It is perhaps impossible therefore to give a representational example of animal metrics. It is this lack of generality that conflicts the most with a human perspective of efficiency.

Recent studies have revealed the sophisticated navigation and landmark recognition skills of individual ants and bees (Collett and Baron 1994; Wehner et al. 1996; Judd and Collett 1998). My findings, that individual ants can make accurate assessments of nest areas based on a rule of thumb, show in a unique way in which animals use robust algorithms to make well-informed quantitative decisions.

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Chapter 5

THE DECISION-MAKING PROCESS

TABLE OF CONTENTS

5.1 Introduction

Social insects have special importance for the study of decision-making, because they make choices not only as individuals, but also collectively. A foraging honeybee decides whether and how much to exploit a given flower patch, based on it quality and on information about colony and environmental conditions (Schmid-Hempel et al. 1985; Eckert et al. 1994). At the same time, her colony as a whole decides how to apportion workers among the many flower patches its foragers have found (Seeley 1995). The collective decision is not a mere summation of choices made by individual insects; the colony can discriminate between two food sources of different quality, even when no single forager has sampled more than one (Seeley et al. 1991). Rather, a global decision emerges from the interactions of many workers, each possessing limited local information, and acting on it with appropriate decision rules.

Most research on collective decision-making has focussed on populous societies with efficient recruitment tools, such as the waggle dance of the honey bee and the trail pheromones of many ant species (Beckers et al. 1990; Seeley 1995; Bonabeau et al. 1997). Large colony size and effective recruitment are important components in the mechanisms of collective action described to date. Recruitment generates critical positive feedback that can amplify small differences among colony options (Beckers et al. 1990). Population size matters because workers rely on rates of interaction with nestmates for indirect cues about colony and environmental state (Seeley 1992; Pacala et al. 1996; Jeanne 1999). Large population size buffers a colony against stochastic effects on, for example, interaction rates that can degrade the quality of information available to each insect.

Decision-making by smaller and less integrated insect societies has attracted much less attention. Many ant colonies, including members of the genus

Leptothorax, number only a few hundred workers, and possess recruitment systems capable of summoning only one nestmate at a time (Beckers et al. 1989). Can these relatively simple societies accomplish the same collective behaviours as more complex colonies, and if so, what are the underlying mechanisms? It may be the case that small colonies instead place a greater cognitive burden on individual workers. However, the actual balance between individual and collective action, and the ways in which these interact, remain open questions. Small colonies offer practical advantages in analysing these questions, because all of the workers can be individually marked, and the behaviour of any given worker described in detail. This approach has successfully been applied to many aspects of social organisation in *Leptothorax* (Franks and Sendova-Franks 1992; 1993; 1999; Franks and Deneubourg 1997)

In this chapter, I will analyse the behavioural mechanisms of nest site selection in *Leptothorax albipennis*. As stated earlier, these ants typically form colonies of fewer than 300 workers and do not produce pheromonal recruitment trails. They nest in pre-formed rock crevices, and must frequently emigrate when their old nest deteriorates or its capacities are outstripped by colony growth (Partridge et al. 1997). In the laboratory, emigrating colonies given a choice between nests of different area, reliably reject nests below a certain size (see chapter 2). I set out to examine how the colony's choice emerges from the behaviour of individual workers.

I have shown that the ants are able to make context-dependent decisions about nest quality, actively comparing the available options and choosing the best one. In this chapter, I will investigate the respective roles of individual and collective decision-making to these choices. I will then analyse the dependence of individual recruitment behaviour on nest quality, and determine how this dependence contributes to the group's decision.

5.2 Methods and Results

5.2.1 Nest preference tests

In chapter two, I showed that the colonies are not satisficing. For example, the nest of dimensions 25mm X 33mm X 1.6mm was considered superior to nests that were half this height (25mm X 33mm X 0.8mm) (section 2.2.5). To ensure that the 0.8mm nest was an acceptable nest, I offered it to the colonies with the alternative choice of a nest of dimensions; 18mm x 23mm with a nest entrance of 23mm. Out of fourteen colonies, all fourteen choose the former nest (binominal test: $p = 0.00006$). Therefore, the 25mm X 33mm X 0.8mm nest is acceptable but mediocre when compared to the nest with the 1.6mm walls. For the rest of this chapter, the 1.6mm nest will be referred to as the superior nest and the 0.8mm nest as the mediocre nest.

5.2.2 Video recording of emigrations

5.2.2.1 Comparison of nests by individual ants

To probe the behavioural mechanisms underlying the colony's choice, Dr. Stephen Pratt and myself videotaped emigrations by colonies of individually identifiable ants. Ants were marked with four tiny paint marks: one spot each on the head and thorax and two on the gaster (Sendova-Franks and Franks 1993). Colonies were then induced to emigrate to nests of different quality, as determined by the results of the nest preference tests. The old nest was placed in a large arena (750 X 430 X 70). On the floor of the arena was placed a large paper grid (50mmX 50mm) Two prospective nests, one superior and one mediocre nest, were placed 450mm equidistant away from the old nest. Removing the roof of the old nest initiated the emigration.

Throughout the emigration, digital video cameras (Panasonic NV-DS1 and JVC GRDV3ek) were trained on the interiors of the new nests. From the

resulting videotapes, we noted for each ant all of her entries, exits, and carrying behaviours. The videotapes did not capture every tandem run, since these often broke up or changed followers in the arena, beyond the camera's view. Hence, we watched the arena and old nest throughout the emigration, recording on the audio channel of the videotape the timing and participants of each tandem run. In total three replicates were carried out. Figures 5.1 a,b,c show the populations and levels of recruitment for each nest type during each replicate. Only in one replicate (colony 1) was there a notable amount of recruitment to the mediocre nest.

I plotted raster plots for all ants that recruited to either nest during these three emigrations. A raster plot shows the time at which each ant began a behaviour. It does not plot when this behaviour ended. Each horizontal line represents a single ant.

In all three emigrations, each nest was visited by many scouts (Fig. 5.2 a, b, c), but recruitment was focussed almost entirely on the better nest. In all, only 12 ants recruited to the mediocre nests versus 119 to the superior nests. Thus worker population increased dramatically only at the better nest, to which the bulk of the colony was moved within two to five hours (Fig. 5.1). The behavioural records of individual recruiters show that this phase of transport ended with a sudden drop in the number of ants transporting (Fig. 5.2). This corresponds to the time when the old nest had been emptied of ants and brood. In Colonies 2 and 3, a trickle of transport continued over the next hour, largely directed at retrieving ants from the arena. In Colony 1, by contrast, this phase lasted for more than two hours. This is because only Colony 1 transported a notable number of adults (16) and brood (13) to the mediocre nest. After the old nest had been completely evacuated, these "misplaced" items were slowly retrieved by scouts from the superior nest (principally ants 1, 14, 19, and 27) (Fig. 5.2a).

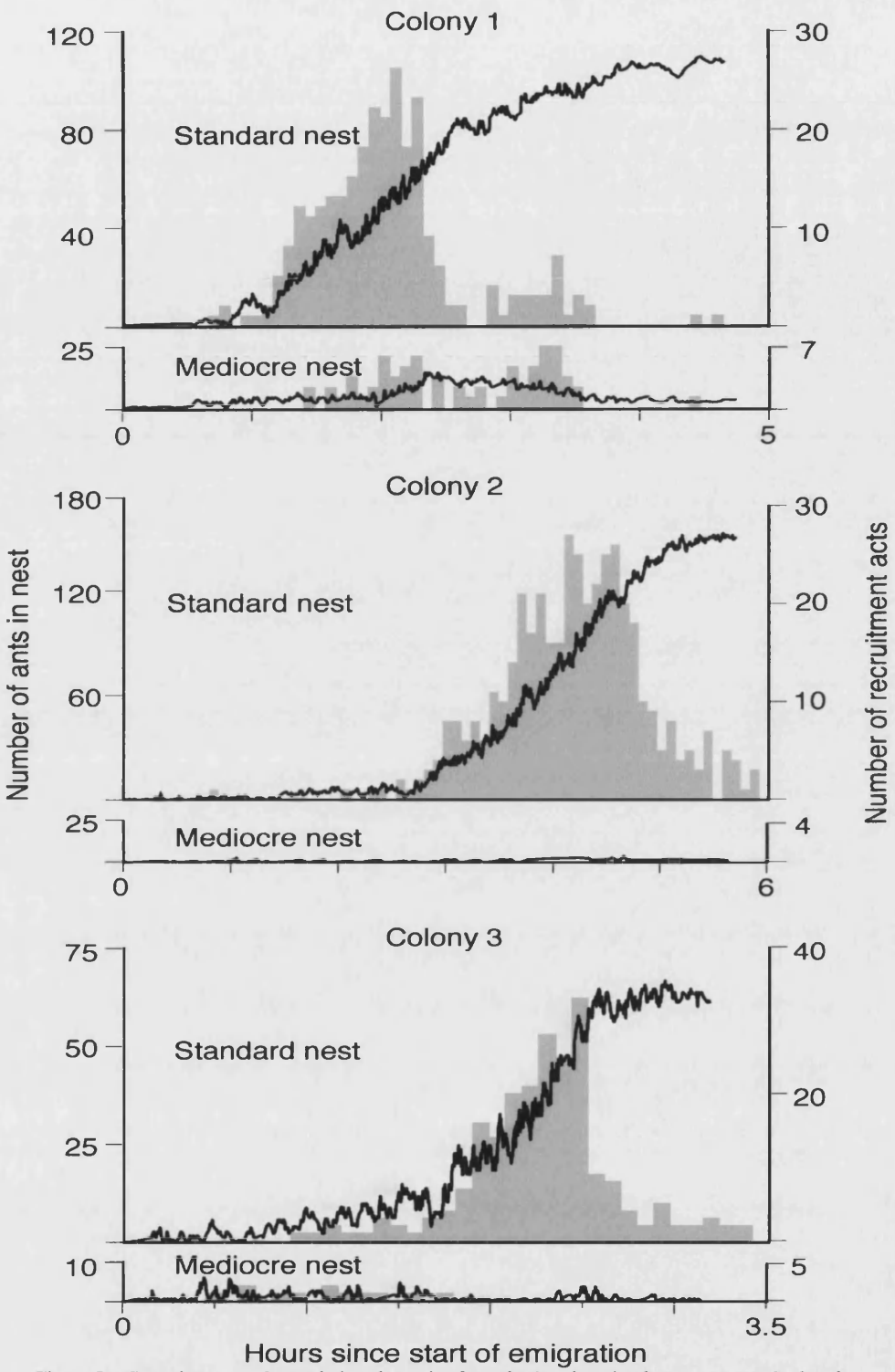


Figure 5.1. Recruitment and population dynamics for colonies choosing between a standard and a mediocre nest. For each nest, grey bars show recruitment acts (tandem runs and transports) and black lines the worker population.

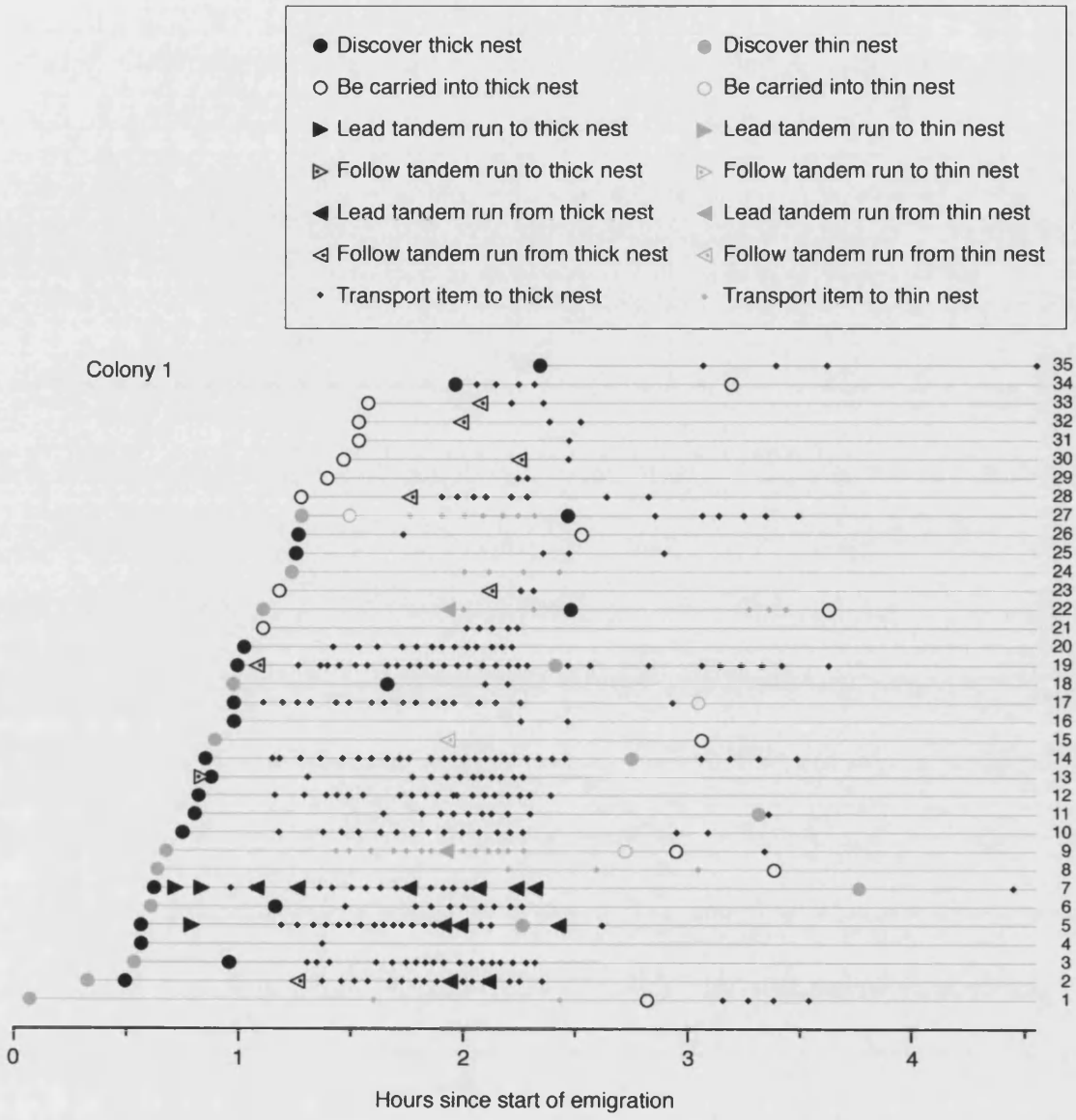


Figure 5.2a. Raster plot of colony 1's emigration. The key for this and the other two raster plots is also shown.

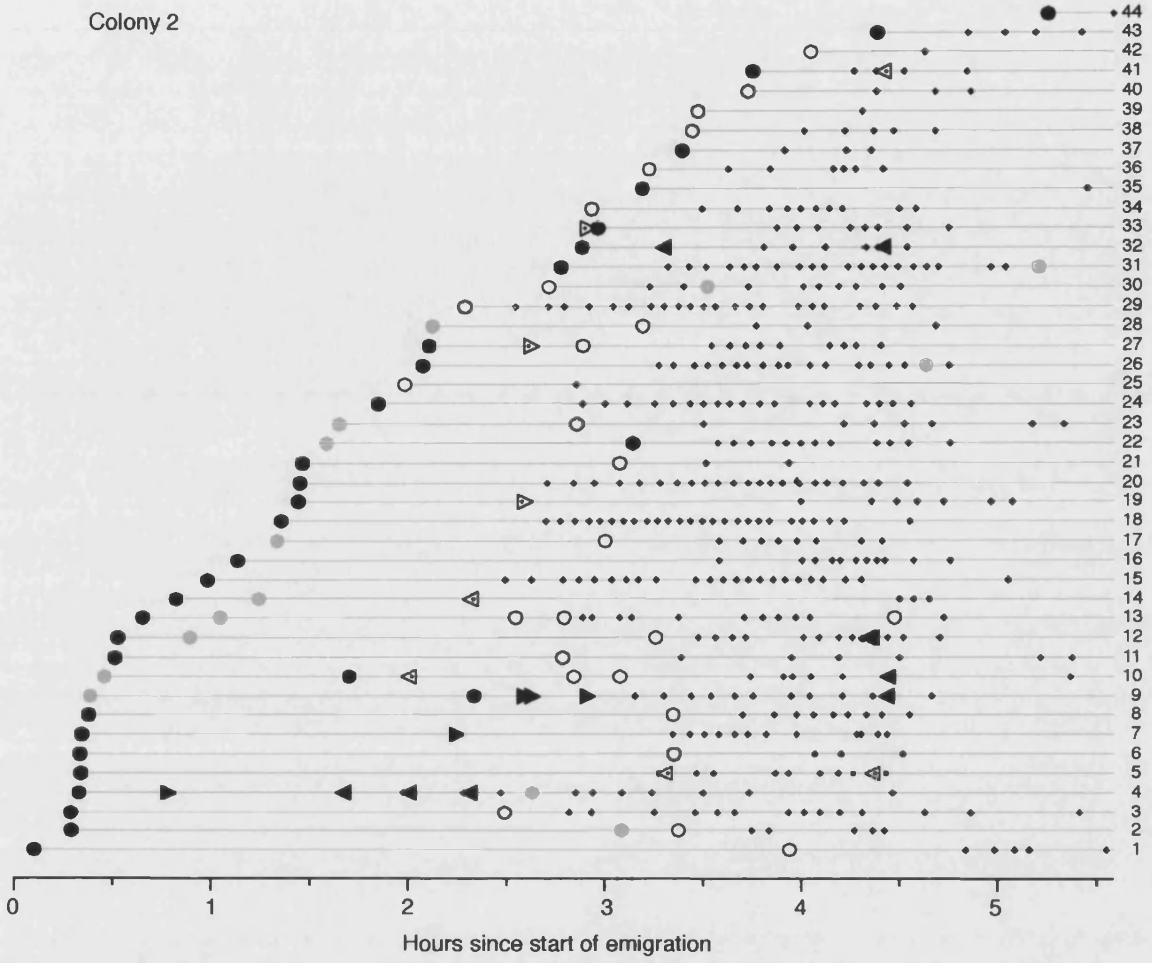


Figure 5.2b Raster plot of colony two

Many scouts visited both nests in the course of an emigration, and thus had an opportunity to compare directly the quality of the nests (Fig 5.3). Of these ants, 37 encountered both nests before beginning to recruit to either of them. If they compare nests and conclude that one is superior, we would expect them to confine their subsequent recruitment to the better nest. Indeed, all 37 initiated recruitment only to the better nest (for example, ants 3, 6, an 18 in

Colony 1; ants 2, 12, and 13 in Colony 2; and ants 2, 4, and 7 in Colony 3) (Fig. 5.2).

A smaller number of ants visited one nest, began to recruit to it, and then discovered the other nest (for example, ant 27 in Colony 1, ant 4 in Colony 2, and ant 28 in Colony 3) (Fig. 5.2). If the ants make direct comparisons, we would expect a discrepancy between the tendency of these ants to switch their recruitment efforts, depending on which nest was found first. Of the ten ants that began recruiting to the better nest and then found the mediocre one, none changed her recruitment target. In contrast, four of the five ants that had been recruiting to the mediocre nest switched their allegiance once they found the better nest. (This calculation excluded ants that performed no

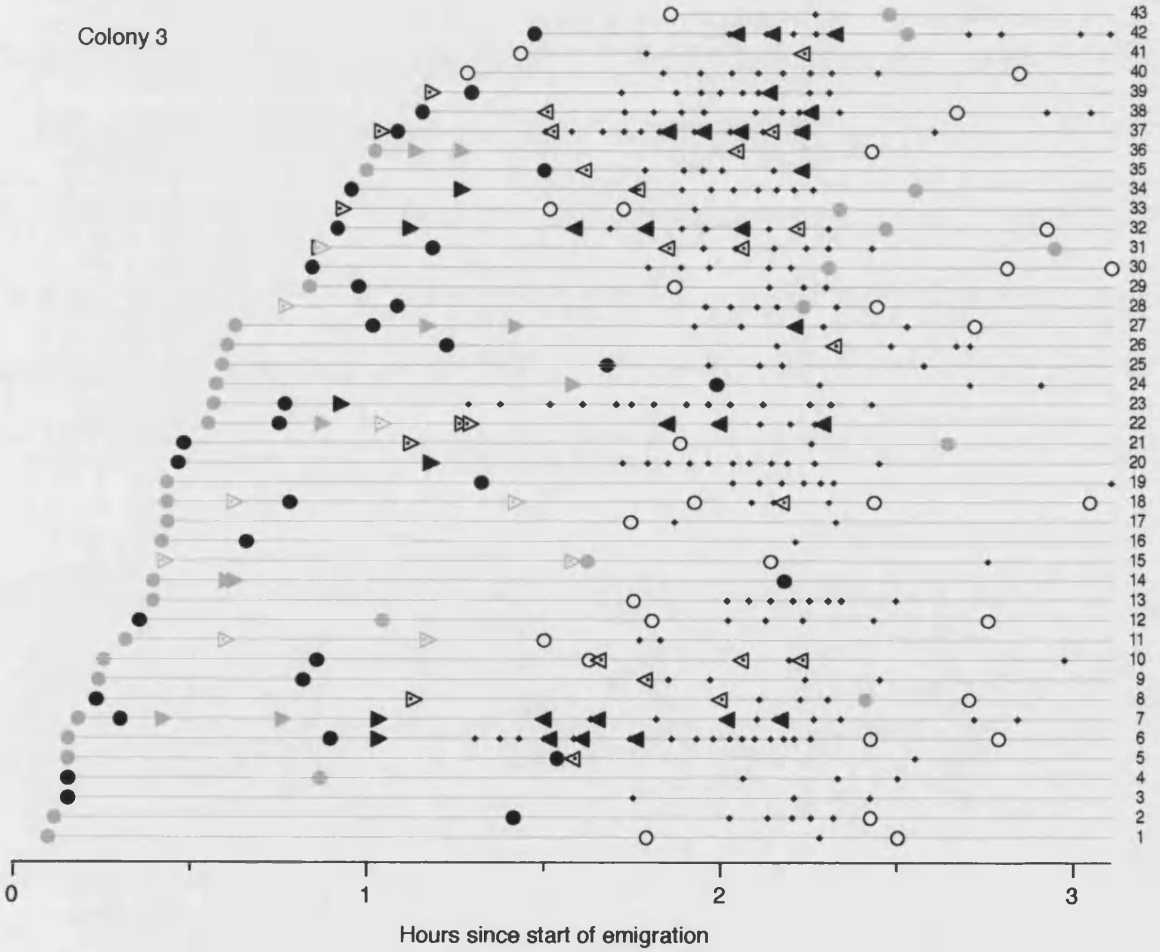


Figure 5.2c. Raster plot of colony 3's emigration

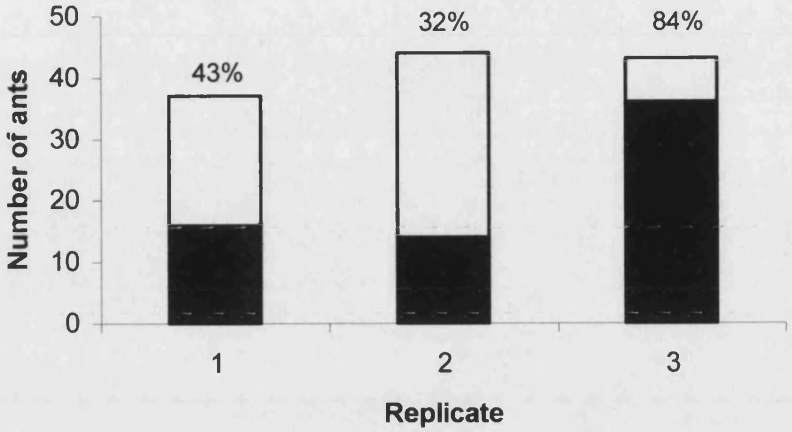


Figure 5.3. Number of recruiters during two camera recordings. The black area of each bar represents the number of ants that visited both the standard and mediocre nests in the course of the emigration. The percentages refer to these ants

further recruitment whatsoever after finding the second nest (for example, ant 31 in Colony 2), since their loyalties could not be determined.) This shows a significant difference between the propensity to switch in these two situations (Fisher's exact test: $p < 0.01$).

It is thus clear that individual ants can compare nests and choose the better one. However, the opportunity for such comparisons varied considerably across colonies (Fig. 5.3). In Colony 3, fully 84% of eventual recruiters visited both nests, but in Colony 2 only 32% did so. In Colony 1 the value was 43%. Thus, two colonies were able to choose the better nest, even with relatively low levels of individual comparison.

5.2.2.2 Influence of nest quality on recruitment behaviour

Scouts that visit only one nest may nonetheless contribute to the colony's decision, if their response to a nest somehow depends on its quality. For example, faster or more intense recruitment to a better nest might allow its population to rapidly overtake that of a poorer nest, even without direct comparison by individual ants. To identify quality-dependent differences in

the behaviour of scouts, I videotaped emigrations in which only one new nest was available. For these experiments, the old nest was placed against the centre of one short wall, and the new nest against the centre of the opposite wall, with a 65 cm separation between entrances. Each of six colonies were induced to emigrate twice: once to a mediocre and once to a better nest. Emigrations were separated by several days, and the order of presentation was randomised across colonies.

I examined four aspects of scout behaviour that might contribute to the effectiveness of recruitment. The number of recruiters was simply calculated as the total of all ants that led tandem runs or transported any nestmates or brood during the emigration. Although this number varied across colonies, ranging from 26% to 48% of colony population, it showed no dependence on nest quality (Wilcoxon signed ranks test: $T = -0.135$, $N = 6$, $p = 0.892$). The recruitment effort, was defined as the number of tandem runs and transports by each recruiter. The recruitment rate was estimated by measuring the duration from the beginning of one recruitment act to the beginning of the same ant's next recruitment act. This interval is the reciprocal of the recruitment rate. Neither of these features differed between emigrations to mediocre and better nests (Tables 1 and 2).

A fourth aspect, recruitment latency, was suggested by differences in the population dynamics at the two kinds of nest (Fig. 5.4). Colonies spend longer exploring a nest before recruiting to it when emigrating to a mediocre nest ($\bar{X} \pm SD = 63.4 \pm 21.7$ min) than when emigrating to a superior nest ($\bar{X} \pm SD = 43.0 \pm 12.3$ min) (paired t-test $t_6 = 2.71$, $p = 0.042$). This led me to consider the time taken by an ant to begin recruiting after first having discovered the nest. From these latencies, survivorship curves were calculated for each replicate (Fig. 5.5). Functions were fitted via the Kaplan-Meier method (Lee 1980) for calculating survivorship curves. Each survivorship curve depicts the rate of

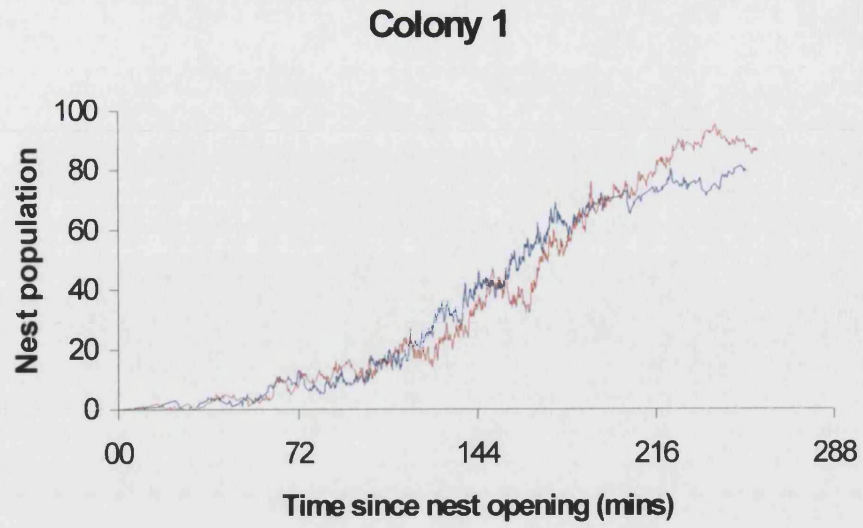
Table 1. The median number of recruitment acts by individual ants did not differ between emigrations to standard and mediocre nests (Mann-Whitney U test).

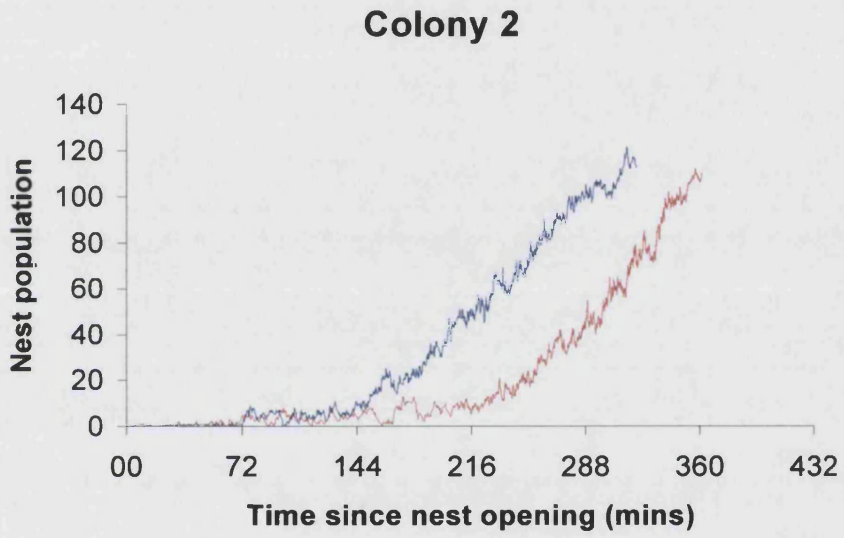
Colony	*Standard*	*Mediocre*	*N(1,2)*	*U*	*P*
1	6	4.5	27,36	873.5	0.9005
2	4	7	51,33	2013	0.1584
3	3	4	37,32	1176.5	0.1556
4	3	5	35,29	1007.5	0.3844
5	3	2	11,20	186.0	0.6855
6	5	5	45,45	2070.0	0.8591

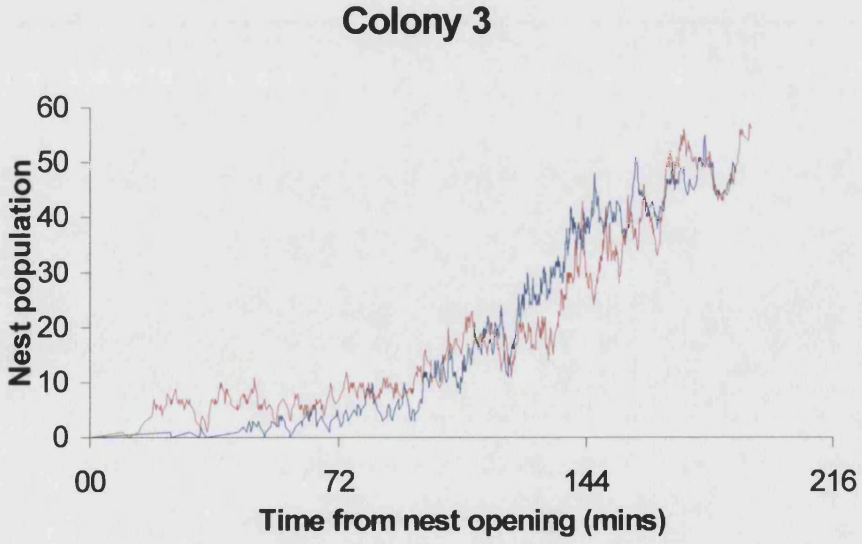
Table 2. The median intervals between recruitment acts for individual ants did not differ between emigrations to standard and mediocre nests (Friedman's ANOVA, 1 df). No results are shown for Colony 5, because it contained no ants involved in emigrations to both the mediocre and the standard nest.

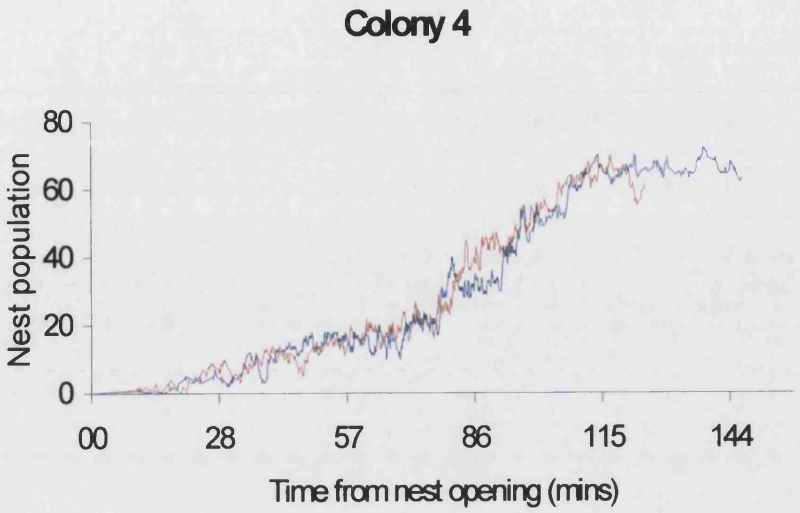
Colony	*Standard Median(sec)*	*Mediocre Median(sec)*	*S*	*n*	*P*
1	417	557.5	4	16	0.046
2	596	521	3.77	13	0.052
3	467.75	462.75	0.08	13	0.782
4	373	391	0.69	13	0.405
6	480	513	1.92	13	0.166

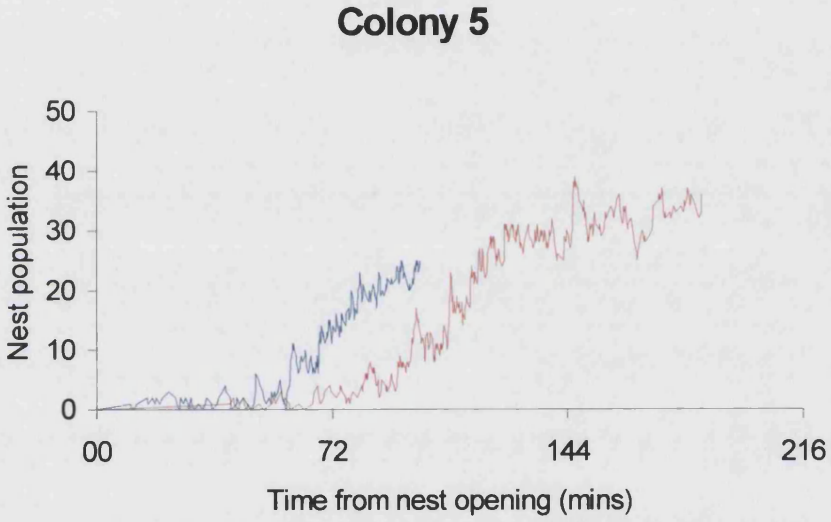
Figure 5.4 Population growth at the new nest during emigrations in which only one new nest was available. Each colony emigrated twice, once to a standard nest (blue lines) and once to a mediocre nest (red lines). Colonies 1-6.

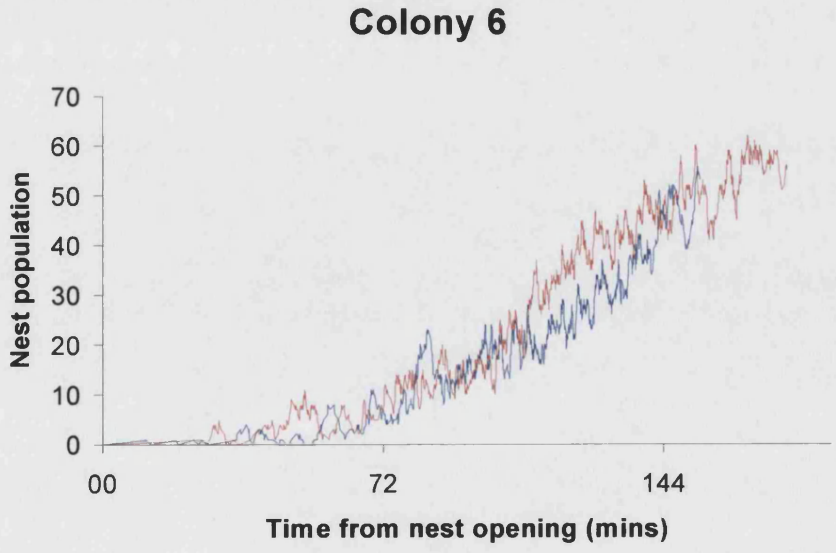

Colony 1
Nest population
100
80
60
40
20
0
00
72
144
216
288
Time since nest opening (mins)


Colony 2
Nest population
140
120
100
80
60
40
20
0
00
72
144
216
288
360
432
Time since nest opening (mins)


Colony 3
Nest population
60
50
40
30
20
10
0
00
72
144
216
Time from nest opening (mins)


Colony 4
Nest population
80
60
40
20
0
00
28
57
86
115
144
Time from nest opening (mins)


Colony 5
Nest population
50
40
30
20
10
0
00
72
144
216
Time from nest opening (mins)

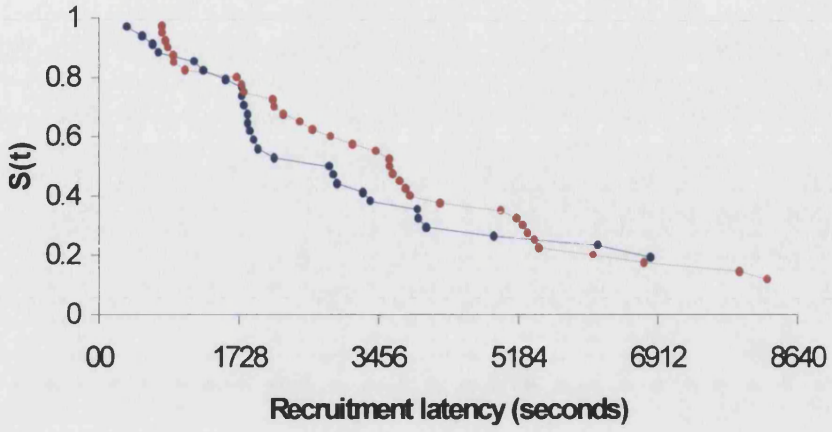

Colony 6
Nest population
70
60
50
40
30
20
10
0
00
72
144
Time from nest opening (mins)

decrease in the population of scouts assessing a nest, as these ants begin to recruit. Because most workers were entirely passive throughout the emigration, we included in the survivorship data only those ants that were potential recruiters. Ants were excluded if they had been carried into the new nest by another ant.

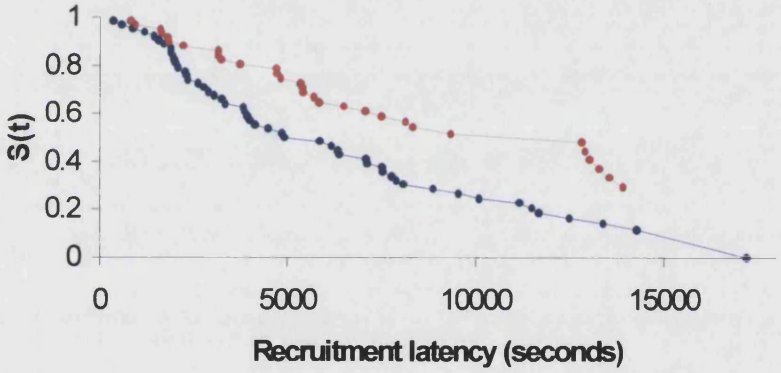
Four of the six colonies had significantly steeper survivorship curves for better nests than for mediocre ones (Fig. 5.5 and Table III). The other two showed nonsignificant trends in the same direction. A steeper slope indicates a higher probability that an ant will begin recruiting at any given time. By approximating these curves as exponential distributions (R^2 ranges from 0.93 to 0.98), we can estimate this probability as the exponential constant. This gives values from 1.32×10^{-4} s^{-1} to 5.02×10^{-4} s^{-1} for good nests and 0.66×10^{-4} s^{-1} to 2.88×10^{-4} s^{-1} for mediocre nests. The mean ratio of the good nest probability to the mediocre nest probability was 1.76 ± 0.63 ($\bar{X} \pm$ SD). Thus each scout arriving at a new nest begins to recruit to it with a probability dependent on the nest's quality.

Figure 5.5 The number of ants not yet recruiting as a function of time since each ant first entered the nest cavity, for the emigrations shown in Figure 5. Functions were fitted via the Kaplan-Meier method (Lee 1980) for calculating survivorship curves. Emigrations to standard and mediocre nests are shown by blue solid and red dashed lines, respectively. The median latency between entry and recruitment is shown in table 3. In four colonies, curves were significantly steeper for the standard than for the mediocre nests, by a generalised logrank test (Lee 1980). The other two colonies showed a nonsignificant trend in the same direction. Steeper curves correspond to shorter latencies and thus to higher instantaneous rates of recruitment initiation.

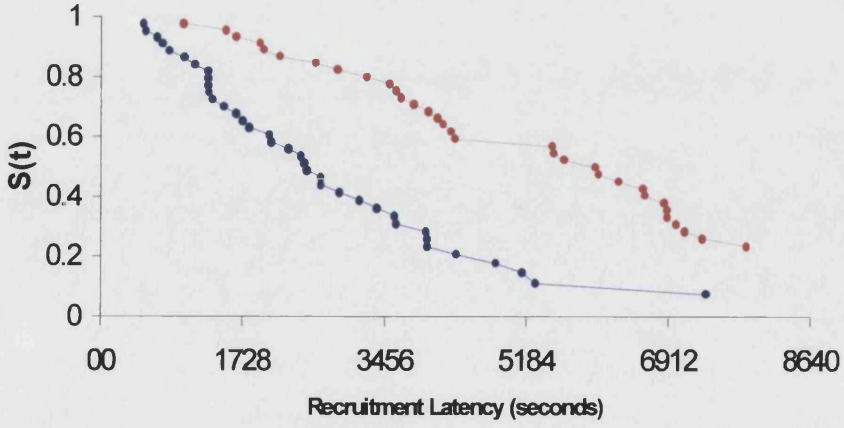
Colony 1



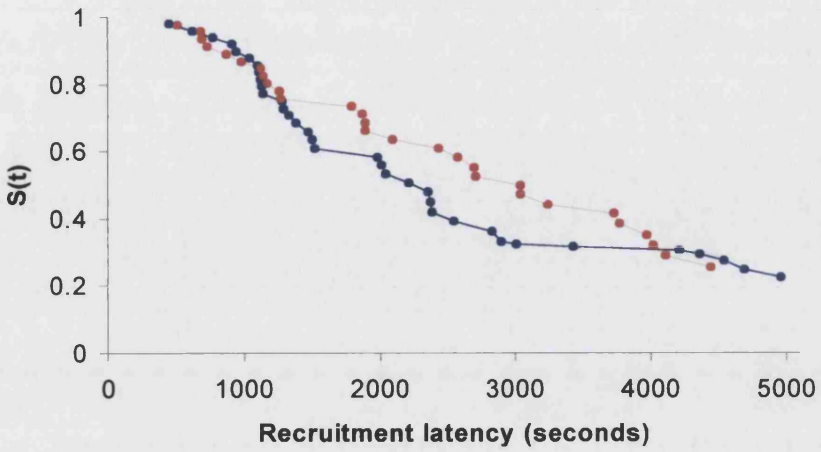
Colony 2



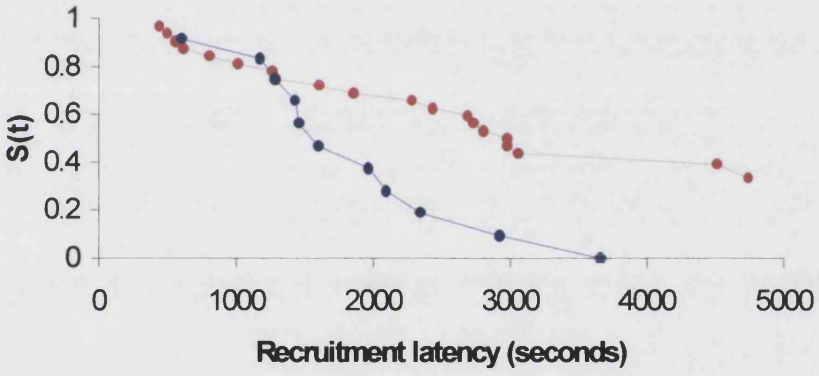
Colony 3



Colony 4



Colony 5



Colony 6

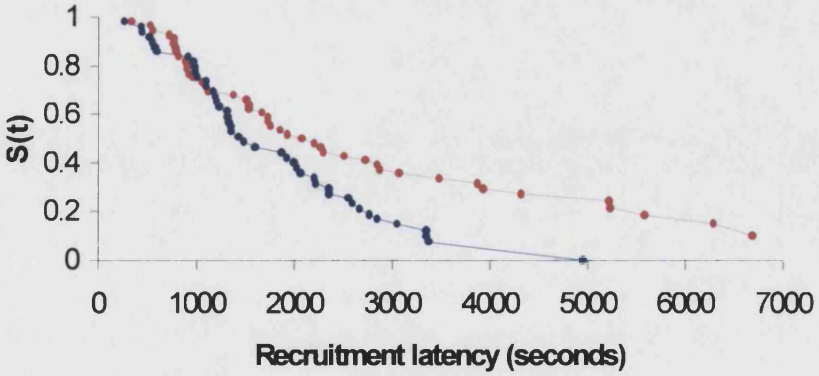


Table III Median latencies for the one camera experiment. The test statistic and probability values are calculated using a generalised Logrank test, a nonparametric method for comparing survival distributions.

Colony	*Superior nest median latency (s)*	*Mediocre nest median latency (s)*	χ^2	p
1	2851	3597	0.02216	0.881
2	5837	12817	10.2052	0.0014
3	2509	6016	17.8632	<0.0001
4	2384	2907	0.07925	0.7783
5	1598	2974	7.3641	0.0067
6	1489	2205	7.3991	0.0065

5.3 Discussion

When offered a nontrivial choice between two nests, colonies of the ant *Leptothorax albipennis* reliably choose the superior one, despite the apparent limitations imposed by their small size and rudimentary recruitment abilities. This decision emerges in part from direct comparisons made by individual scouts that have visited both nests. However, the colony can choose the better nest, even when most scouts visit only one of the alternatives. These less-informed ants also contribute to the decision, because they take less time, on average, to initiate recruitment to a superior than an inferior nest. This difference underlies positive feedback that drives up recruitment to better nests more rapidly than to worse ones. I propose that the colony's decision emerges from a combination of this distributed process, and the ability of some ants to make direct comparisons.

Chapter 2 showed that in making their choice, colonies do not merely satisfice, taking the first option that surpasses a threshold quality. Under such a strategy, statistically half of the colonies should have chosen the mediocre nest when it was offered with the superior one. The mediocre nest was clearly judged acceptable by the ants, because it was strongly preferred to a still-smaller nest with a larger entrance. Nonetheless, when a better nest was available, the ants unambiguously preferred it to the mediocre design. Two important conclusions about the colony's decision follow from these results. First, the ants somehow integrate several aspects of nest design, rather than depending on a single key characteristic (chapter 2). Second, they take into account not only each nest's intrinsic qualities, but also its worth relative to the available options.

How does the colony's decision emerge from the behaviour of individual workers? On theoretical grounds, small colonies might be less likely than large ones to use distributed decision mechanisms. For example, large colonies

sometimes partition a task across two or more groups of workers, each specialising in a portion of the task (Jeanne 1986). A proper allocation of workers to each subtask is required so that no one faces undue delays waiting to interact with members of another group. These queuing delays grow exponentially with decreasing colony size, because small colonies experience greater stochastic fluctuations in the arrival of individuals (Anderson and Ranieks 1999). Thus small colonies may benefit from making individuals responsible for the entire task burden.

Nest choice by *L. albipennis* appears in part to bear out this generalisation. In contrast to most studies of decision making in social insects (Beckers et al. 1990), we found that individual scouts can and do compare alternative nest sites. Still, many recent studies have shown how relatively simple cognitive mechanisms can underlie apparently complex behaviour (Bonabeau et al. 1997). Might a similarly simple mechanism lie behind the comparative abilities of *L. albipennis* workers?

A hypothesis of this sort is suggested by the distribution of recruitment latencies: i.e., the intervals between an ant's first entry into a nest and her first recruitment to it. For a given nest quality, this distribution is approximately exponential, with a rate constant that gives the probability per time step of initiating recruitment. When an ant discovers two nests of different quality, we can imagine that two independent exponential processes continue in parallel. The ant eventually chooses whichever of these first ends with a recruitment act. More often than not, this will be the better nest, because of its higher rate constant. This would occur even though the ant is not directly comparing the nests, but merely treating each just as she would if it were the only one she had found.

On the basis of this mechanism, I calculated the proportion of ants discovering both nests that are expected to recruit to the inferior one:

$$P(X_s < X_m) = \frac{1/\bar{X}_s}{1/\bar{X}_s + 1/\bar{X}_m} \quad \text{(Ross 1993)}$$

$\bar{X}_s$ and $\bar{X}_m$ are the median recruitment latencies for the superior and inferior nest. These values were estimated as 63.7 and 82.5 min, respectively, from the twelve emigrations described in section 5.2.2.2. For an exponential process, the instantaneous probability of an ant beginning to recruit does not depend on how much time has passed since she discovered the nest. Thus the relative timing of the discoveries of the inferior and superior nests can be ignored. Under this model, of the 29 ants that discovered both nests before beginning to recruit, 16.4 should have chosen the superior nest and 12.6 the mediocre one. These numbers differ significantly from the observed values of 29 and 0 (χ^2= 20.5, 1 df, $p < 0.00001$). Therefore we can reject the hypothesis that the ants treat each nest independently. They appear instead to compare them actively and choose the better one.

One further possibility is that the number of ants already in the nest could influence the decision of these scouts. This is very likely. However, it does not negate the possibility that the individual ants can choose between nests when given the opportunity. The issue of whether individuals are making a comparison does not depend on the criteria on which they base it. The criteria can be the physical characteristics of a new nest or the number of nest mates in it or a combination of these.

I attempted to isolate the effect of the number of ants in the new nest on the recruitment latency of the scouts. There tended to be a negative correlation between these two variables. However this is an artefact. Early-arriving ants can have short latencies or long ones, but later arrivals can only have short ones (Figure 5.6), because their assessment periods are terminated by the end

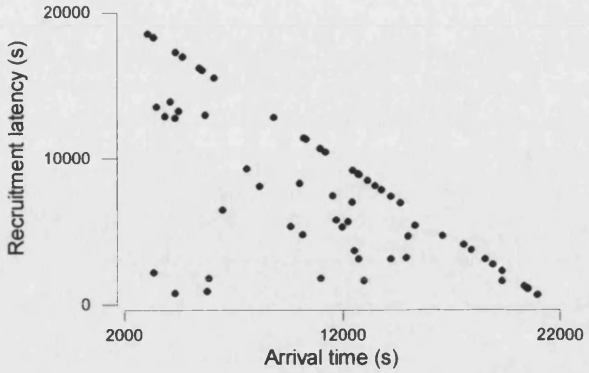


Figure 5.6 Recruitment latency against the time from the beginning of the experiment and the arrival of the ant. Note the lack of high valves as the experiment draws to a close.

of the emigration. The question of whether the new nest population does influence the scouts is an interesting one. However, I can not answer it from the data that I have collected.

A possible avenue would be to compare the recruitment latencies of a colony's scouts to a standard nest and the same colony's response when some ants are artificially moved into the new nest before the beginning of the experiment. The number moved in could not be too many, so that it not just replicate the situation at the end of an emigration, that is the cutting short of latencies due to the end of emigrations.

Allowing for the individual comparison of nest sites, this still cannot completely explain the colony's decision-making. In my three choice experiments, two colonies chose the better nest, even though a majority of their recruiters visited only one nest. The third case, in which over eighty percent of the recruiters saw both nests, may not be the most typical situation in nature. By offering only two nests in a small arena, I probably increased the number of independent discoveries of both nests, relative to that expected in a larger and more complex natural environment.

The bulk of poorly-informed scouts still contribute to the colony's choice, through a distributed process reminiscent of decision-making in large-colony species. A crucial ingredient in these cases is the dependence of recruitment strength on target quality (Detrain et al. 1999). This allows positive feedback to amplify small differences in individual assessment of a target, even in the absence of direct comparison by scouts. For example, *Lasius niger* deposit more pheromone on recruitment trails to better food sources (Beckers et al. 1993), and honey bees encode food quality by the duration of their dancing, which feeds forward into the number of bees recruited (Seeley and Towne 1992).

In *L. albipennis,* the number of recruiters, the rate at which they work, and the amount of work performed by each does not depend on nest quality. Instead, the difference lies in each ant's likelihood of initiating recruitment to a site. In essence, scouts impose a time penalty on recruitment to a worse nest. Some of this delay is undoubtedly due to the need to assess the nest's quality, but there is no reason an inferior nest should take longer to assess than a better one. Rather, the delay appears to underlie a colony-level strategy for increasing the likelihood of choosing a superior nest. Slowing down recruitment to worse nests not only buys time in which to find more candidate nests, but also assures more powerful positive feedback on recruitment to better nests. At the same time, because recruitment eventually begins even to a poor nest, the colony avoids barring itself from any new nest, if nothing better is available.

Besides choosing the best available nest, colonies must also ensure that their decision is unanimous; at the end of the process the entire colony should be moved into a single nest. For *L. albipennis*, this requirement is probably seasonal, because colonies spend much of the spring and summer divided among several nests (Partridge et al. 1997). Still, for the rest of the year, only a unanimous decision will preserve the colony's unity. This requirement

separates nest site selection from foraging decisions. Honey bees, the only other society in which house-hunting has been studied in detail (Lindauer 1961; Camazine et al. 1999; Seeley and Buhrman 1999), seem better equipped to reach unanimity than *L. albipennis*. The bees clearly separate decision-making from emigration, with the bulk of the colony taking flight only after a small group of scouts have settled on a single nest. The ants draw a weaker distinction between choosing and moving. It is entirely possible for a colony to transport passive workers and brood to more than one nest simultaneously. If these nests differ in quality, then the longer recruitment latencies for the inferior nest should, on average, minimise the number of ants ending up there.

The weakness of this method is that parts of the colony may be stranded at inferior nests, because nothing prevents simultaneous transport to several sites. If this happens, the colony must enter a subsequent phase of transportation among the new nests to bring everyone to the best one. This entails additional costs in time and energy, as well as prolonging the risky exposure of colony members to the outside environment. This occurred in one of my emigrations (Colony 1). One response to this danger may be the intriguing "reverse" tandem runs seen during the transport phase of emigration (Figure 5.3). These lead from the new nest back to the old, and probably function more generally to direct transporters to any site where lost nestmates need retrieval (Pratt *et al.* in prep.).

The ants may also act proactively against splitting by using the previously mentioned rule for switching from tandem running to transport. Recruiters make this switch only if a sufficient number of other ants have already arrived at the new nest. This rule can do more than simply ensure an adequate number of transporters. By delaying the start of the rapid transport phase, it interposes a deliberative period during which scouts arrive at a decision about the nest. In essence, each ant takes a "poll," supplementing her own

evaluation with an indirect cue about the evaluations of other ants. This imposes a longer delay for inferior nests, because ants arriving there are less likely to initiate recruitment and drive the population above the transport threshold.

That the switch in recruitment type marks a critical decision about the new nest is also supported by the timing of reverse tandem runs, which occur only during the transport phase. Tandem run behaviour can be summed up by assuming that each ant has a nest designated as "home" and only leads tandem runs from this home to a place where assistance is required. Early in the emigration, the old nest is still home, and scouts use tandem runs to summon help in evaluating a potential new nest. After the switch, the new nest has become home, and tandem runs now direct transport effort toward brood or adults who need retrieval (Pratt *et al.* in prep.).

The decision-making behaviours I have described combine elements of individual and collective choice. It is tempting to conclude that the relatively prominent role for individual comparison stems from the small size and simple organisation of these societies. It is possible, however, that the aforementioned need for a unanimous decision is also relevant. House-hunting honey bees show evidence of both individual comparison and distributed decision-making when searching for a new home. Most scouts visit only one candidate site during the decision phase, but a small number see multiple sites (Camazine et al. 1999; Seeley and Buhrman 1999). It is not clear, however, that direct comparison is necessary for a correct colony-level decision. In a simplified experimental choice between two identical sites, colonies reached unanimity even when scouts who have seen more than one nest were prevented from returning to the swarm (Visscher and Camazine 1999). However, in a more complicated natural situation, with dozens of potential sites of varying quality to sift through, there may be a significant role for even such a small amount of individual comparison.

In *L. albipennis*, we cannot yet determine whether the ability of individuals to make direct comparisons is functionally important to the colony. However, recent work on foraging decisions suggests potential advantages of using a mixture of behavioural mechanisms. Ants that rely only on mass recruitment with trail pheromones are well able to settle on the better of two available food sources, but are not always able to switch their efforts if a better source is later discovered (Beckers et al. 1990). Species that combine mass and group recruitment show greater flexibility in this situation (Beckers et al. 1990). This is because a small number of group recruiters can overcome the powerful positive feedback exerted by odour trails which otherwise locks the ants into their first choice. Indeed, a similar role for small numbers of especially active or well-informed "instigators" has been proposed for the design of intelligent systems based on co-operative swarms of agents (Numaoka 1995). In general, groups may gain both greater flexibility and robustness by combining different behavioural tools to meet a given information processing challenge.

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Chapter 6

CONCLUSIONS

This thesis describes my efforts to determine how *Leptothorax albipennis* colonies assess new nests and choose among alternatives when their old nest has been destroyed. Have I been successful? What has been learned from this study?

A surprise finding was the way in which individual ants measure the area of the nest. I found that they were deploying individual specific pheromones during their first of multiple visits to the nest. When ants crossed over these paths on subsequent visits, they briefly slowed down. It is thought the ants are assessing the rate of intersections between their current visit path and the trail they laid down during their first visit. This rate is inversely proportional to the area of the nest, paralleling the logic of a classic exercise in mathematics known as Buffon's needle problem. I showed that this algorithm would produce highly accurate estimates of nest area.

The colonies do make consistent decisions about what type of nest to inhabit. They consider many different variables. These variables are integrated to give a single value for that nest as viewed by that ant. This integration of different variables takes place at the level of the individual scout. The quality of the nest is represented by the individual scouts as their probability of recruiting to a nest after they have examined it.

Many scouts will have assessed many different nests. How does this nest-quality dependent probability of recruitment lead to a unanimous decision by the whole colony to emigrate to the higher quality nest? It is due to the much quicker buildup of ants at the better nest. Ants that are lead to a superior nest by tandem run are in turn more likely to begin recruitment themselves. Recruiters make the switch from tandem running to carrying only if a sufficient number of other ants have already arrived at the new nest (Pratt *et al.* in prep.). This rule can do more than simply ensure an adequate number of transporters. By delaying the start of the rapid transport phase, it interposes a deliberative period during which scouts

arrive at a decision about the nest. In essence, each ant takes a "poll," supplementing her own evaluation with an indirect cue about the evaluations of other ants. This imposes a longer delay for inferior nests, because ants arriving there are less likely to initiate recruitment and drive the population above the transport threshold.

Can the suite of behavioural rules described above really account for decisions made at the colony level? An agent-based model currently in development (Pratt *et al.* in prep.) suggests that they can, but it also highlights the need for behavioural complexity at the individual level. For example, when simulated ants cannot make comparisons between the relative quality of their "home" nest and another nest, the colony will sometimes remain split between two candidate sites. In most cases such a comparison is unnecessary, but it is required if a unique choice is to be ensured. The potential importance of each individual's ability to make comparisons contrasts with the oft-quoted examples of pheromone following by foraging ants, where positive and negative feedback mechanisms are enough to yield a collective decision (Beckers *et al.* 1990). If so, this may reflect the great importance during nest site selection of arriving at a single, colony-wide decision. Combined with the use of two distinct recruitment mechanisms, and a context-dependent switching rule between them, this indicates a greater role for individual cognition in decision-making by these ants, compared to large colony species. For these ants, it is the mixture of feedback-based rules and some higher individual cognitive abilities which makes possible an optimum collective decision.

It is interesting to me, how through the course of this thesis, the abilities of the individual have come to the fore. It is the individual ant that assesses the nest. It is the individual who converts all the different aspects of a new nest into a single measure of quality. Individual comparisons of nests, whether they are based on

nest quality or a census of ants in the new nest, are numerous and probably quite important. Often in the recent past of social insect research, the individual ant, bee, wasp or termite has been seen and modelled perhaps too literally as the mindless agent that were originally and appropriately invoked when self organisation theory was first applied in physics and chemistry. Often in our attempt to explain social insect colonies as the latest major transition in evolution, we have drawn too many parallels between the components of other evolutionary groups (organelles, cells etc.) and the individual social insect. A large difference between these groups and social insects is the ratio of communication to computation (Seeley 1993). These other groups are often physically connected and therefore communication between the members is relatively cheap allowing computation to be truly distributed. Social insects have no physical connections (Wilson 1971) and therefore the burden of computation must be on the individual. This thesis shows how complicated the individual ant can be and is a warning to us social insect biologists to ignore this complexity at our peril.

List of contributions

- First elucidation of the quality dependent response of *L. albipennis* scouts to nest sites of different qualities.

- First synthesis of the previous contribution with earlier discoveries of the temporal organisation of an emigration. It is the combination of quality dependent recruitment and a two speed emigration process (Tandem runs-slow; Carrying-fast) that leads to a collective decision.

- First evidence of the ability of scouts to individually compare nests of different qualities. This is thought to be of importance in ensuring that decisions are unanimous.

- First discovery of the novel method by which *L. albipennis* scouts measure the area of a new nest.

- First evidence that these ants are using individual specific pheromones within a nest cavity.

- An attempt to catergorise formally the decision-making strategy used by an animal.

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